

GEOGRAPHICAL VARIATION OF MANIOLA JURTINA (L.)
(LEPIDOPTERA, SATYRIDAE)

by

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ABSTRACT

The form and geographical variation of the male genitalia of *Maniola jurtina* are described and the distribution of the various types encountered is examined. An analysis of the structure is combined with a close examination of the possible evolution of the species. The morphological and genitalia correlations are studied, forming the basis of a revision of the sub-species and geographical races of *jurtina* in which two new sub-species are described.

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1. INTRODUCTION

Possibly there is no more familiar butterfly species than the Meadow Brown (*Myrtill* in France, *Ochsenaue* in Germany, *la Loba* in Spain, *Almän Slättergräsfjäril* in Sweden and *Bruin Zandoogje* in Holland) nor one which is more welcome, heralding the appearance of summer, at least in central and northern Europe. In spite of this (or perhaps because of it) a full understanding of the species has evaded the few specialists who have given it some attention, the consequence, no doubt, of lack of material or, more commonly, a lack of objectivity in assessing the relative value of *jurtina* characteristics. Work in some major areas has still to be begun, notably larval variation and host plant associations, cytology, temperature and humidity effects and the genetics of most of the wing markings.

As much taxonomically important information on the species was collected (Thomson, 1969) to serve as a basis for further study, but the shortcomings of the resulting paper were no doubt as well known to the author as to anyone. Work from that time continued with increased enthusiasm to such an extent that, with the acquisition of a number of representative series, several long unresolved problems have now been tackled and to a great extent these have been solved. The appeals of Lempke (1935) and Pionneau (1936) for a study of the French *jurtina* were not taken up by any entomologist in or out of that country. Now, thanks to the generosity and co-operation of a number of French colleagues,

what I consider to be a satisfactory organisation of the French races of *jurtina* has been completed. In other regions such as north-west Spain, north Africa and even Iran, a much clearer picture than that which existed before has been built up.

Without doubt, many of the answers came directly or indirectly from a study of the genitalia. This work, inspired by that of Dr. L. G. Higgins, was both time consuming and extremely rewarding. What originally seemed to be an enigma, namely the apparent lack of correlation between the genitalia and known phenotypes, turned out to be the key to an understanding of the geographical forms of *jurtina*. It is, perhaps, rather surprising that so little notice has been taken of the work of Le Cerf (1912, 1913) on the genitalia of the species. Although it is nearly sixty years since his details were published of the differences between the male armature of the eastern part of the butterfly's range (*persica* and *ghilanica*) and what he called "*jurtina*", "*hispulla*" and "*fortunata*", authors of countless papers and articles in the entomological literature continued to report "form *hispulla*" from the eastern part of the species range. However, even Le Cerf was deceived by the fact that the material he considered to be *jurtina* came from an intermediate region and, had he examined the genitalia from British or east-Swedish insects, he would have indeed been surprised by what he saw. In fact his *persica* genitalia were of the typical eastern type (usually called *jurtina*).

Muschamp (1915) observed that the genitalia of what he called *jurtina* and the southern European *hispulla* Esper differed from each other, although his record of the discovery was decidedly misleading:

'.....I am inclined to believe that the valve is not exactly the same in the southern var. of the species; the valve of *hispulla* is blunter and more squared off in almost every case.....'

In the first instance he did not say from where in the "south" his material came, which, in the light of recent investigations, would render such details essential and, secondly, because of the form of the valve it is difficult to know what he meant by "more squared off". Nor does his illustration help as he failed to say whether or not the drawing of the *jurtina* armature (which I suspect derives more from imagination than science) represents the "southern var."

So the situation remained until 1950, when Professor Gustaf de Lattin (1950) claimed for *hispulla* specific rank. Furthermore, he realised that the Turkish insects were not a *hispulla*-form and that *hispulla* was restricted to the western Mediterranean. H. de Lesse (1952) restated de Lattin's views separating *hispulla* as a good species and illustrating the structure of a specimen from Seine et Oise (France) as *jurtina* which, being of what had come to be known as the *hispulla* type, showed that even he did not fully understand the nature of the valve variation. De Lattin (1958) published additional information in the form of a distribution map, but the limits of the ranges of the valve types do not correspond with what has since been found.

Details of the supposed distribution of the genitalia types were given by Bernardi (1961, 1966) who confused the issue somewhat as he obviously did not fully appreciate the individual variability of the structure and, having based his results on only a few mounts (probably only one or two — although he does not say), came to some rather strange conclusions regarding speciation in the genus *Maniola*. The scientific value of his work on the butterfly is so reduced by his inadequate sampling that it will be necessary only to deal with certain aspects of it in the relevant sections of this paper. Bernardi

believed that the distribution of *jurtina* (*hispulla*) extended from the Canary Islands and North Africa through the Iberian Peninsula to south France and including the Balearic Islands, Corsica, Sardinia, Sicily and Malta. The remainder of the species range, and also Corsica, he said, was populated by the species *janira* with the exception of that occupied by *megala* which he considered to be distinct.

Important and extensive work was recently undertaken by Higgins (1969) who claimed that the range of the western or "old *hispulla*" genitalia was much more westerly and northern, than had been presumed, extending from the Canary Islands, through north Africa, Sicily, Corsica, Sardinia, south and west France to Great Britain. The eastern (*jurtina*) type, he reported, was found in Finland to Austria, Italy and eastwards. Between the two regions he found an area in which they meet and fuse.

Dr A. F. Tauber (Vienna) has recently studied the species in "the east" (1968, 1969, 1970) and his work has raised some interesting questions, but, like Bernardi, his samples were inadequate although there are indications of another zone of secondary intergradation in Turkey. A paper on this subject is in preparation.

Clearly, it was necessary to find out more about the true nature and extent of the variation of the *jurtina* genitalia, particularly relating to the known geographical forms of the species. My previous work on the species completely ignored the structural variation of the genitalia, so from 1969, until the time of writing, I have undertaken an extensive examination of the structure throughout its range, from Finland in the north, to the Canary Islands in the south and from the Irish Arans in the west, to the southern shores of the Caspian Sea in the west. This paper is the result of that work. In it I have related the structural variation to that of the known phenotypes. In the taxonomy I have gone to much trouble to avoid name changing and the proliferation of taxa in this already "over described" species. Some older taxa (e.g. *mirtyllus* Fourcroy) have been resurrected to this end. Possibly the most controversial arrangement is the acceptance of Verity's decision about the type locality of *jurtina* and thus the typical sub-species which has so often been cited as Sweden. This has necessarily meant the reintroduction of the name *janira*. However, some specialists have over the years accepted the type locality restriction of Verity, including De Lattin, Bernardi and no less an authority than Hemming (1958), so, in this respect, I am not proposing an entirely original solution. Furthermore, it leaves the name *fortunata* Alpheraky available for the Canary Islands form, should this be considered necessary. The total taxonomic change thus consists of the reintroduction of two 'older' taxa, the sinking of a single taxon as a junior synonym and the description of two new subspecies.

Perhaps more than with any other familiar species *jurtina* has suffered from a galaxy of taxa unaccompanied by adequate descriptions. I have, therefore, included detailed descriptions of races where these are not already readily available or where the original or subsequent descriptions are misleading.

Acknowledgement is due to so many people who have helped in some way with this work that I can only mention a few and trust that in the case of the others my appreciation is understood. Special thanks go to R. F. Bretherton, E. C. Pelham-Clinton, R. L. Dickson, T. G. Howarth, J. H. Robert, A. Valletta, the Royal Scottish Museum and the British Museum (Natural History) for the supply and access to specimens and information, also A. Finnie who took most of the genitalia photographs for this paper.

2. METHOD AND MATERIAL

Slide mounts

Because of the structure of the male valve in the *jurtina* group it is somewhat difficult to make more than very general comparisons of its shape, size and proportion by the usual optical methods. The structure has been described by Muschamp (*loc.cit.*) as very irregularly shaped for a Satyrid, being "made up of concave and convex hills and valleys". I have attempted to rationalise the dimensions of the structure by the usual three-dimensionally mounted genitalia, but without success. It was discovered, purely by accident, that a much simpler approach to the problem would yield the results for which I was searching. This method is now described.

The male genital armature of *jurtina* is comparatively exposed. Removal of the valve — the right valve was used in this research — can be simple and quick from both fresh and dry specimens, although both have minor drawbacks which require some care to be taken. These are, however, of no real significance if one is aware of them. If the specimen is freshly killed, light pressure applied to the sides of the abdomen will expose the genitalia. The valve to be removed can be pulled out further with fine pointed forceps, when it will normally remain in an exposed position. A pair of fine dissecting scissors are inserted, one blade between the two valves, and the other between the valve to be removed and the hairy valve cover as far to the rear of the structure as possible. The removed valve should be handled as little as possible and it is best if it falls directly onto the slide. When the desired position on the slide is achieved a cover slip is placed on it without pressure, this being applied only when the two sides of the cover slip are taped. Mounting the valve from fresh specimens has the disadvantage that the liquids which exude from the structure can be troublesome if they obstruct vision, but it is seldom serious in extent. To remove the valve from a dry specimen a pair of very fine pointed forceps are inserted closed between the two valves which are carefully separated. The valve to be removed is gripped firmly by the forceps and gently broken off as far back as possible. This will nearly always be at the valve's junction with the ninth segment (vinculum). It is mounted on the slide in the same way. Mounting dry has the disadvantage that occasionally the structure cracks when pressure is applied to the slip. However, as with the mounting of fresh individuals, the wastage rate is very low.

The large number of mounts required for the study of the valve variation could have been undertaken only by this method in reasonable time. About thirty or forty preparations can be made in an hour.

Photographic

The use of a photographic enlarger to make permanent records of temporary mounts of the androconial scales in *Pieris* has already been suggested (Thomson, 1970a). A much more sophisticated approach can be used with valve mounts giving remarkable results if care is taken with focus and exposure. Photographic prints have the advantages that they can be examined under any conditions without the microscope; several can be compared at the same time and they take up much less storage space than conventional mounts. Furthermore, it will be seen in the main part of this paper that accurate measurements can easily be taken from these "micro-photograms" in a way which would be

difficult or impossible otherwise. In the case of a Satyrid valve the enlargement required is small, $\times 12$ being convenient for most work, although $\times 18$ would produce better results if a greater degree of accuracy was required. The enlarger is set using a transparent or translucent scale so that the desired magnification is uniform and repeatable. The focus is carefully checked. This will remain constant provided the mounts are on the same thickness of slide. For most work any orthochromatic bromide paper (grade two or three) is adequate. The criterion is whether or not details other than the outline of the structure are required. Occasionally the dorsal edge of the *jurtina* valve is 'turned over' and a false impression of the shape would be obtained if this went unobserved. The chitinous exoskeleton is of a reddish colour, making longish exposures necessary with orthochromatic materials, thus losing some of the internal detail and the 'hairs' which are so characteristic of the structure. This can be overcome by using panchromatic paper (e.g. Panalure of Kodak), although one must work in darkness or inconvenient panchromatic lighting conditions. Using bromide paper produces a white image on black, but this could be reversed by projecting first onto film, using the negative to produce a positive print. However, this adds nothing to our knowledge of the valve and I do not see any real value in this form of reversal unless considerable magnification is required.

In spite of the variability of the valve large samples as are necessary when studying the wing markings in the species are not necessarily essential, as the nature of the population is usually clear after looking at only a few mounts. This is not so in the zone of secondary intergradation and, although a sample of ten to fifteen was considered adequate for pure eastern and western types, a larger number of twenty or thirty had to be measured if considerable variation was detected.

Collection and samples

The material came from a large number of localities throughout the *jurtina* range, but very few from its eastern part from where specimens are, for political or geographical reasons, very difficult to obtain. A special sample series was taken on our trip across France in 1970 (Thomson, 1970c) to correlate east-west longitudinal direction to the change in the valve form. Together with the material, collected by colleagues and friends in France and Belgium, it was possible to plot the change in both the north and the south of that country. In total in excess of eight hundred male valves were mounted and measured from eighty nine localities, while about ten thousand *jurtina* were examined, many in great detail, in the preparation of this paper. The specimens were in my own collection, private collections and in the Royal Scottish Museum, Edinburgh.

3. THE MALE GENITAL ARMATURE

Description

An exhaustive description of the male genital armature would be superfluous here, as this can be found elsewhere (Le Cerf, 1912, 1913; De Lesse, 1952). Variation occurs in the brachia (gnathos), the aedeagus and to a greater extent in the valves tending towards one of the main forms in Europe and the Near East with an intermediate ("blend") zone. A third form is found in Iran and the extreme east of Turkey. These types will be called

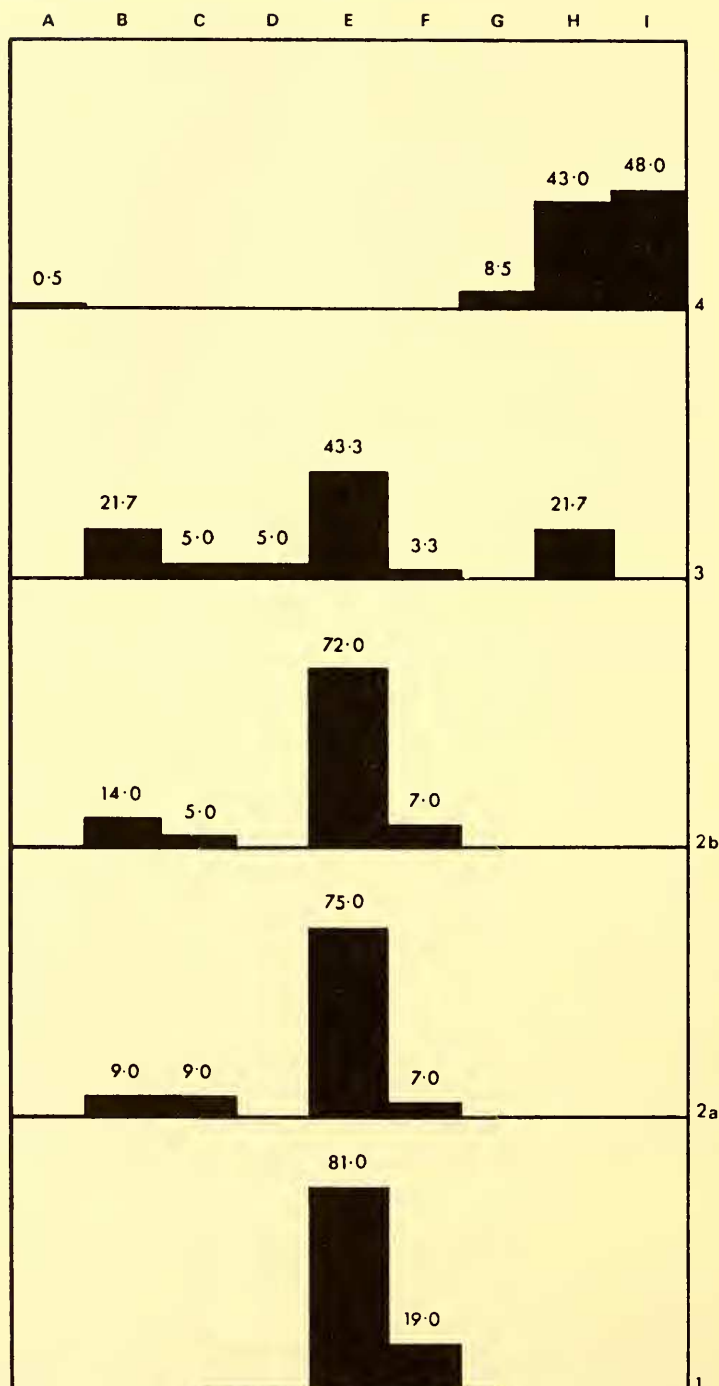


Fig. 1. The relative proportion of valve types in *Maniola jurtina* in: 1. south west (North Africa, Spain, Portugal, Balearic Islands, Malta and southeast France); 2a. west France; 2b. Britain; 3.

Fig. 1. The relative proportion of valve types in *Maniola jurtina* in: 1. south west (North Africa, Switzerland, Germany, Hungary, U.S.S.R., Italy, Crete, Corsica, Finland, east Sweden). A — relict primitive; B — relict transitional type a; C — relict transitional type b; D — secondary transitional; E — western type a; F — western type b; G — eastern type a; H — eastern type b; I — eastern type c

eastern type (*jurtina* sensu Higgins and *persica* Le Cerf) and the primitive type (*ghilanica* the western type (*bispulla* sensu Higgins and De Lesse and *fortunata* sensu Le Cerf), the Le Cerf). It should be noted that Le Cerf's "*jurtina*" is intermediate in character. These three types are figured. For an interpretation of some of the terms which I have used in the following description (see page 23 and 27).

WESTERN Type (Pl. 1 Fig. 11).

Brachia markedly swollen at the base to almost twice the width of the "neck" of the uncus. Aedeagus slightly swollen at its extremity. Valve usually moderately large, rarely very large. Dorsal edge moderately long, sometimes very long and nearly always strongly concave. Dorsal process variable but always longer than its width at its extremity, frequently almost pointed or sharply rounded but sometimes with a short flat top. Dorsal edge, dorsal process and distal edge to the distal process smooth and free from irregularities. Ventral edge usually strongly convex and sometimes forming an acute angle with the distal edge.

EASTERN Type (Pl. 1 Fig. 10).

Brachia narrow and gradually tapering to their extremity without marked swelling at the base; narrower at the base than the "neck" of the uncus. Aedeagus straight, with little or no swelling towards the extremity. Valve variable in size and proportion ranging from very long (in the south) to very short (in the north). Dorsal edge usually short, rarely strongly concave. Dorsal process very short and broad, nearly always flat-topped and much wider than its height, but occasionally rounded, to form a long convex curve to the distal process. The dorsal edge, dorsal process and distal edge to the distal process more or less irregular. Ventral edge gently convex, only occasionally strongly curved.

PRIMITIVE Type (Pl. 1 Fig. 9).

Brachia narrow and gradually tapering to their extremity without marked swelling at the base; narrower at the base than the "neck" of the uncus. Aedeagus straight with little or no swelling towards the extremity. Valve rather large. Dorsal edge usually very short, hardly ever strongly concave. Dorsal process very short and broad, nearly always flat-topped and wider than its length. The distal edge of the dorsal process to the distal process (which is rather long) is decorated with a "fringe", variable in extent, but very irregular outwardly. This fringe appears to be attached to the outer surface of the valve. Ventral edge convex, but only slightly so.

It should be noted that a fringe-like structure is present in some, but by no means most, eastern valves. Although it is likely that this structure is homologous to that found in the primitive type, its manifestation in most cases demonstrates their differences more than their similarities. In the case of the eastern form the position of the fringe on the valve is extremely variable, occurring anywhere from the distal process to the inner edge of the dorsal process, occasionally appearing in other parts of the valve surface and other unrelated areas. While the eastern type valve is more usually without it, the western type sometimes, but infrequently, shows evidence of this unusual feature. The primitive type

always has a fringe which is quite clearly an irregular appendage to the distal edge of the valve.

Comparison with other *Maniola* species

It is extremely interesting to relate the form of the genital armature of *jurtina* to the other *Maniola* species: *telmessia* (Zeller), the insular *nurag* (Ghiliani) from Sardinia and *cypricola* (Graves) from Cyprus. In all three species the valve is much closer to the western type, although in *telmessia* there are some traces of an intermediate element. The frequent misconception that *telmessia* lacks the "Jullien Organ" should be cleared up here. These structures are, in fact, always present in *telmessia* but they are much thinner and more easily removed than those in most *jurtina*. Examination under the microscope will reveal, in cases where the genitalia appear to lack the "organ" that they have been knocked off, either in nature, or in the preparation of the mount and the point from which they have been removed will be seen quite clearly. I have encountered one such individual *jurtina* from London. Specimens of *telmessia*, apparently lacking these structures, occur frequently enough, so that Verity described race *telmessiaeformis* as a form of *jurtina* which resembled *telmessia* in all respects, except that it had the "Jullien Organ". The explanation for this is now quite clear. The evolutionary implications of the valve form in these species will be discussed later.

4. VALVE VARIATION

Valve types and their distribution

The variation in the shape of the *jurtina* valve is considerable by any standard, yet, in spite of this, it is relatively easy to recognise the primitive, eastern, western and even transitional types when these occur. Furthermore, similar, if not identical, forms occur frequently enough, not only in the same locality but in widely separate areas, so that it has been useful to classify these according to the form of the dorsal process, in order to be able to refer to them later. These main types are figured. The reasons for my use of terms "primitive", "secondary" and "relict" in this context will become clear in the ensuing discussion.

primitive type (Pl. 2, Fig. 1) — dorsal process distally edged with an extremely irregular "fringe", usually extending to the distal process and apparently attached to the outer surface of the valve.

relict primitive type (Pl. 2, Fig. 2) — more or less similar to the primitive type and distinguished from others by the presence of the "fringe", but the body having an outline more or less like that of the eastern type. (Bernardi illustrates the *janira* type as having a "fringe" or crest attached to the inner surface of the valve. As I have said, this feature is inconsistent in the eastern type and occurs rarely in the western. The irregular dorsal and distal edge should not be confused with this).

relict transitional type a (Pl. 2, Fig. 3 and 4) — dorsal process rather short or short and broadly rounded, with little or no flattening at its extremity.

relict transitional type b (Pl. 2, Fig. 5) — dorsal process very short and almost or sharply pointed.

- secondary transitional type (Pl. 2, Fig. 6) — dorsal process long, with a rather broad, flat top.
- western type a (Pl. 2, Fig. 8) — dorsal process long, with a more or less rounded extremity.
- western type b (Pl. 2, Fig. 7 and 9) — dorsal process long, with a pointed or very sharply rounded extremity, or with a short flat top.
- eastern type a (Pl. 2, Fig. 10) — dorsal process distally forming a long convex curve to the distal process. (This is the type found in ssp. *megala* by Bernardi and used as evidence for raising the status of the race).
- eastern type b (Pl. 2, Fig. 11) — dorsal process fairly short with a flat or almost flat top.
- eastern type c (Pl. 2, Fig. 12) — dorsal process very short with a long flat top.

A long examination of the valve types in localities from which material was available, indicated that the distribution of the eastern and western types broadly coincided with that described by Higgins, although the limit of the western range was rather further east in France and the transitional region probably a little less widespread than previously thought. The only notable point of difference was that the genitalia type in Corsica was transitional and not western. What was considerably more interesting was that there appeared to be a consistent difference between the populations of north Africa, Spain, Portugal and south-east France and those of western France and Britain. The relative proportion of the valve types in the latter group was virtually identical. A histogram showing the proportion of the various valve types in each region is given (Fig. 1). It is worth noting that the composition of the western populations is similar in terms of the relative proportion of each of the western types and that the west French and British samples differ from the southern group in the presence of the relict transitional elements. This distribution of types is also found in the transitional zone where eastern, as well as western forms are found.

The distribution of the primitive type is difficult to ascertain, not only because of the few collections which are made in Iran and eastern Turkey, but also because in this part of the world *jurtina* is both very local and, at least sometimes, quite uncommon. It is almost certain, however, that it is the most restricted of the three main types. It is also unique in the fact that, from the slim evidence available, there is no transitional locality similar to that found between the eastern and western zones. Populations in the East in which this valve type occurs are composed entirely of them.

Although the presence of a primitive type valve as a rarity within the eastern range would seem unlikely, two such forms turned up at Verbier in the Swiss Valais and Cortina d'Ampezzo in north-east Italy, two high altitude localities. The significance of this is increased by the discovery of the relict transitional valves within the western zone. These were first thought to be eastern types, but a closer examination of them, in the light of my investigations as a whole, made it obvious that they were, in fact, indicative of the insect's evolution.

There are, therefore, five main population groups:

1. the south-western — north Africa (with the Canary Islands), Spain, Portugal, the Balearic Islands, Malta, south-east France and probably also Sardinia. In this region the "pure" western genitalia are found substantially free from relict transitional elements.

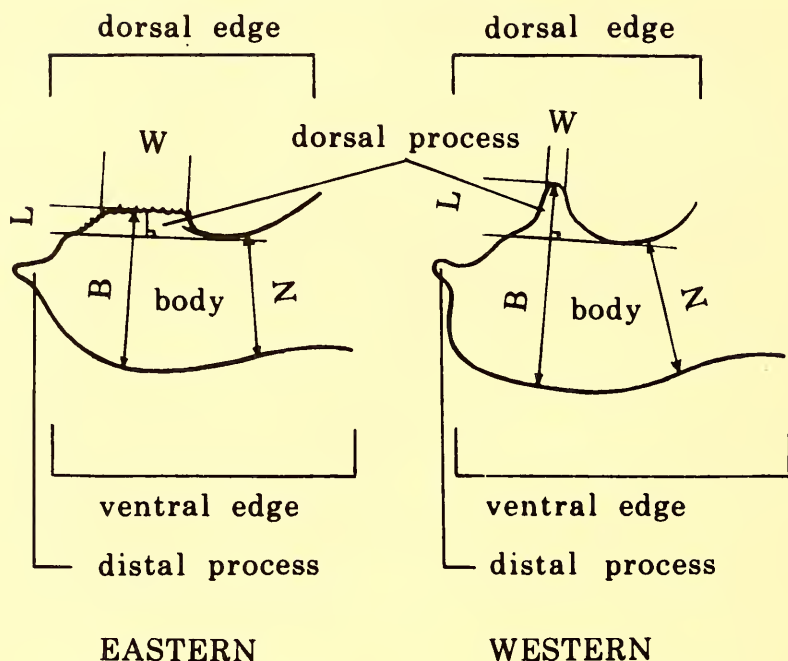


Fig. 2. Diagrammatic representation of the two main *jurtina* valve types, showing terms used and measurement parameters.

By far the most common valve type is the western type *a*, followed by type *b* which comprises about one fifth of the population.

2. the west French and British — France north and west of the Cevennes to Brittany bordering on the transitional zone to the east, and all of the British Islands. Here the relict transitional elements are found as a very small part of a basically western zone.

3. the transitional — west Sweden, (presumably Norway), Denmark, the Netherlands, Belgium and France, east of a line running from the Pas de Calais, just east of Paris to the Franco-Italian border on the Mediterranean coast and Corsica and bounded to the east by the Alps, Jura, Vosges and the Ardennes. In this complex region western, eastern and transitional types occur in more or less equal proportions. Most frequent are the relict transitional, western type *a* and eastern type *b*.

4. the eastern — east Sweden, most of Germany, Switzerland, Italy, and eastward throughout the range of the species excluding the region occupied by the primitive type.

5. the primitive — north-east Iran, the Elburz Mountains and south-west shores of the Caspian Sea, (possibly to) north-east Turkey. Only the primitive type valve occurs.

The distribution of the valve types is shown in Map 1.

Explanation of the valve distribution

The *Maniola* species *cypricola*, *telmessia* and *nurag* are so much an integral part of the evolution of *jurtina* that they are considered here as the result of a single evolutionary event. Although no explanation of the ancestry of our insect fauna can be free from doubt or criticism, I can think of no other explanation of the development of these species

that would fit the facts better than that which I am about to detail.

Without the presence of occasional genitalia types which I have called "relict transitional" in the west and "relict primitive" in the east, it would be very difficult indeed to say with any degree of certainty how the present distribution of the valve types came about. As it is, it would be difficult to explain the presence of such forms in such widely separate localities as Scholes (Yorkshire, England), Banstead Downs (Surrey, England), Falais and Bordeaux (France), if it were not that these individuals do, in fact, represent relict elements of a past fauna and that the western type genitalia were more recent than the eastern. Similarly, the presence of what I call the "primitive" valve in the eastern range substantiates this claim and gives us a good indication of the way in which the structure has developed. From this I deduce that the race or races of the mountains of Iran are the oldest surviving ancestors of the insect, from which *jurtina* has come — possibly a montane species. The eastern races which possess the primitive valve, fly at an altitude of about two thousand meters and frequently well over it. It is worth noting that the relict primitive valves so far found were from montane localities, Verbier, at 1500—1750 m (probably the highest locality in western Europe) and Cortina d'Ampezzo, at 1250 m. There are few places in the western range where *jurtina* flies at high altitude, but it can be taken at 1650 m in the Atlas Mountains in Morocco. The highest western type locality in western Europe, from which I have specimens, is Mt. Ventoux, Vaucluse (France) taken at 1250 m. The Col du Tende (Alpes Maritimes) at 1450 m is a transitional locality.

If we accept that the species has come from the east, we are faced with the question of how *telmessia* and *cypricola* have evolved there with western type genitalia, but I believe that this gives us the key to the solution. I have come to the conclusion that *jurtina* travelled westwards in two streams, originating either east of the Caspian Sea, or, what is more likely, from the area we now call Iran. The more northern migration moved westwards, either north of the Caspian Sea, or from Iran north over the Caucasus then westwards. The other took the southern route through Iran. The structure at this time could well have looked much like the primitive type we now know. While the northern stream extended its range very slowly westwards evolving little, the southern stream, favouring the warmer conditions, probably spread quickly through Iran, Turkey, south Greece (and the land mass now remaining as the Greek Islands), Sicily, Corsica, Sardinia, north Africa and the Canaries to Spain, west France and Britain evolving very rapidly to a type much like the relict transitional. However, an isolated group established itself north of the Elburz Mountains — what we now call *ghilanica* — retaining the primitive valve and genitalia. When Cyprus, Rhodes and Lesbos were split from Turkey and Angiastri from Greece, the western type valve had almost fully developed. The northern stream continued its slow westward spread, probably interrupted by frequent glaciations, to the Alps, south into Italy and north to Scandinavia. A branch which had already evolved the eastern type genitalia, swung into Greece and across the Bosphorus to Turkey. Here it met and dominated the western type, except for a few individual populations which had developed to such an extent that they were able to retain their identity as *telmessia* and in another form, as *cypricola*. This stream might well have also met the relict races of north Iran, but these were able to survive to this day. Meanwhile, the southern stream had evolved the western characteristics particularly in Spain and north Africa where they were isolated by the Pyrenees. A most important event then took place: the western types spread eastwards, meeting what had now developed into the eastern types which were moving westwards,

forming a zone of secondary intergradation in the region in which we now find the two types and intermediates flying together.

Maniola nurag could well have evolved sympatrically with *jurtina* on Sardinia or it could have been the result of two waves of migration, the first having evolved specifically, before the second arrived.

Although this explanation assumes that there was access to the west and to the north of the Black Sea (possibly over the Caucasus) and also through Turkey, the Aegean Island area, Sicily, probably at a time when peninsular Italy did not exist, Sardinia, Corsica, north Africa, across the Strait of Gibraltar, to the Iberian Peninsula, France and Britain, it does largely follow the routes of the Siberian and Oriental migrations. The situation in Corsica introduces a problem as the island would have to have been connected to continental Europe and Sardinia, something about which morphogeologists disagree. However, morphological comparisons confirm these suggestions very well. I suggest that *nurag* is the furthest development of the *jurtina* ancestor. This is based on the fact that the valve is purely western in form, the fulvous on the upperside of the butterfly is very extensive and it was thought that it was the only *Maniola* species capable of producing a second brood, although only under artificial conditions (Simmons, 1930), but I successfully produced a brood of *jurtina* in February 1973, from eggs laid in August 1972, simply by providing the larvae with a continuous supply of their foodplant. This would also explain the similarities between the south-western races and those of Britain and support my claim that the British races are closer to each other than to the *jurtina* of the low Countries and Sweden.

5. NUMERICAL INTERPRETATION OF THE VALVE FORM

Measurement of the valve

The necessity for finding an objective approach to comparing *jurtina* valves might not be obvious as, excepting a few intermediates, it is possible to say whether a specimen has a valve of the eastern or western type without much difficulty. The nature of the eastern, western and transitional distribution in western Europe is such that a much more intensive study of the structure's form could yield valuable information about each of these zones and their relationships to one another. It is important to remember that the valve of the species is unusually variable in shape, size and proportion. The overall size of the valve varies quite independently of the size of the insect of which it is part. Fig. 2 shows a diagrammatic version of the "typical" eastern and western types which roughly represent the two more widespread forms occurring in the species. The long "hairs" which are characteristic of the structure have been omitted for clarity. This outline is only a little different from what would be seen in a conventional genitalia mount, as the whole structure has been slightly flattened. Normally this distortion is uniform in all mounts made: abnormal distortion can be easily detected by the presence of cracking or overlap. For the purpose of this work various parts of the valve have been named and this is indicated on the figure. Also, conveniently abbreviated terms for the parameters from which measurements have been taken are given.

Measurements were taken across the narrowest part of the body from the dorsal edge to the ventral edge (N), also across the broadest part from the top of the dorsal process to the ventral edge (B). The method of determining the length of the dorsal process (L)

and its width (W) is described later. At first it was thought that the difference between B and N would give an accurate measurement of the length of the dorsal process, but it was soon realised that the occasional sample in which the valve was markedly tapering distally gave quite misleading figures. Neither N, nor B gave useful data on their own and were abandoned as part of the analysis. Similarly, the distal process, even within the same locality, was so variable that it was considered an unusable character.

The simple difference between the process length (L) and the process width (W) was by far the most useful algorithm giving consistent results, although it presented a problem of accurate measurement. For the most part it was a simple matter to measure W as the dorsal process usually "squares off" slightly at its extremity. However, the occasional specimen turned up in which it was so rounded that an educated guess was the only answer. Fortunately, this nearly always happened in the western type when the process was long and narrow and the effect of such individuals on the result can be considered negligible. More difficult to describe than to measure is the method by which the process length was determined. The edge from the distal process to the top of the dorsal process, which is basically concave, nearly always has a slightly convex part indicating the start of the dorsal process. A line is drawn at a tangent to the convex dorsal edge to this point. L is line. Occasionally no convex section can be detected in which case the line is drawn from mid-way between the distal and dorsal processes.

All figures given for the valve dimensions, are in millimeters, taken from an enlargement of twelve times. The actual size can, therefore, be simply calculated if comparisons are to be made between my figures and those taken from a magnification, different from that used throughout this work.

Extensive examination and measurement of the structure showed that the algorithm L-W gave in numerical terms an accurate representation of the nature of the valve.

When $L - W > 0$ the valve is of the western type.

When $L - W < 0$ the valve is of the eastern type.

The reason for taking a difference rather than a ratio was purely for convenience in working with smaller figures and positive and negative values, representing the western and eastern types, respectively. However, as will be seen later, the ratio $\frac{L}{W}$ was used in the calculation of variability co-efficients.

Statistical

The following conventions are used:

$F = L - W$ (i.e. the difference between the process length and the process width)

$$R = \frac{L}{W}$$

n = sample size

It was desirable to calculate from the data the following values for each sample:

- 1) the mean (M)
- 2) the range (r)
- 3) the standard deviation (sd) being the square root of the sum (\sum) of the squared deviations (d) from the mean (m), divided by n

$$\text{i.e. } sd = \sqrt{\frac{\sum d^2}{n}}$$

- 4) the co-efficient of variability (cv) being the standard deviation expressed as a percentage of the mean. For this the ratio (R) was used

$$\text{i.e. } cv = \frac{\text{sd (of R)} \times 100}{m}$$

6. STATISTICAL STUDIES

General distribution patterns (Map 2)

The measurement and analysis of resulting data from eighty-nine localities was not without its problems. Not least were the localities in which the values of F for the samples did not fit a developing pattern, or one which was anticipated. Such were places like Scholes (Yorkshire, England) (0.5), Coleraine (Co. Derry, Northern Ireland) (0.9) and Rabat (Morocco)(1.3) which gave remarkably low figures and Serignac (Gard, France)(2.5) and Cramond Island (Scotland)(2.3) which gave unusually high values. At first these results were suspected and in such cases checks were made with a larger sample which invariably confirmed the original figure. The presence of the rather low figures in the west can be explained as another manifestation of the relict theory which I proposed for the occurrence of relict types in the west. Admittedly, the rather high values present us with an anomaly.

The 1.8 recorded for Santander in north-west Spain might at first seem incongruous until one considers the geographical position of the area, cut off by the Cantabrian Mountains to the south. This area is inhabited by a number of species which have developed distinct characteristics. In the case of *jurtina* the form there resembles that of south-east France more than anywhere else in Spain. This has been confirmed by the form of the genitalia.

In general, however, a remarkably clear pattern resulted and there was an extremely good correlation between the figures for adjacent localities. This was tested by comparing two samples from Surrey, one from Banstead Downs and the other from Ashted Heath. In the case of the Ashted sample the value of F was 1.1, while that of Banstead was only 0.2 different at 1.3. In general, the value of F increased to the south and west and decreased to the south and east, reiterating what was already observed in the broadening out of the transitional zone in the north, with a greater gap between the eastern and western forms in the south than in the north.

West - east analysis and the nature of the transitional zone

To determine more accurately the nature of this east-west variation, a special sample study was made of the value of F in two series of selected sites, to relate the change in the mean value of longitudinal direction. In addition to the mean the standard deviation and range were used to build up a picture of the variation. In the south it was possible to use a set of eight samples from localities lying along a straight line from Santander to the Col du Tende ranging from 43 to 44 degrees north. In the north, the west - east line ran from Falais (Calvados) to Verbier, taking a southern turn at its eastern end and ranging from 49 to 46 degrees north. The necessity for using material from localities along this line was in spite of the fact that a special effort was made to collect samples for this purpose. It would have been desirable to continue the set of figures further into the

eastern range, particularly in the south, but material was not available.

The figures which resulted from the measurements and calculations are represented in the population range diagrams (Fig. 3 and 4). Therein can be seen the very real differences between the east-west transition in the north and south. Not least of these is the consistently higher variability in the north. Indeed this was so great that if one *sd* was represented on either side of the mean it would have extended beyond the range in some cases. Furthermore, the range itself was greater in the north, in some examples plummeting to a very low negative value. In the south the range never dropped below zero at the minimum end of the scale. More important, perhaps was the difference in the nature of the two sample series. The northern transition is characterised by an erratic but definite decrease in the mean west to east, accompanied by an increase in the standard deviation, while in the south there is virtually no change in the mean west to east, nor is there any real change in the *sd* from Santander to St. Valier, thereafter followed by a sudden drop in the mean and increase in the variability.

Another illustration of the broadening of the transition zone to the north can be seen if we relate the drop in mean to the west-east distance in both samples. Taking the distance from the most easterly western sample to the eastern limit of the transition zone, we find that in the north the drop from Feucherolles (Seine et Oise, France) to Besançon, a distance of 400 km is 1.0. This compares with the distance of 60 km from St. Valier to the Col du Tende where the drop in mean is 0.7. It is difficult to say whether or not there is an eastward decrease of the mean within the transition zone, but indications are that this is so. One single point of interest is the sudden drop in variability at Verbier, indicating the apparent isolation of the eastern type from even the transitional zone at this point. The *cv* at Verbier was only 20 which compares with between 30 and 40 for localities within the western range and 80 to 90 for the transitional localities. The *cv* of 123 in the Cretan samples was unexpected, however.

The effect of altitude

Adequate material to determine the effect of altitude on the valve was not available and only tentative remarks can be made from the samples examined. No two adjacent localities which varied significantly at altitude were studied. Verbier (1500 - 1750 m) and Ivrea (800 m) are more than a hundred kilometers apart and Cortina d'Ampezzo (1200 m) is half that distance from Bolzano (262 m). These were the closest localities from which any indication of the altitude effect could be obtained and from these it would seem that it had little or none. Rather than altitude having an effect on the valve's structure as such, it has probably acted more as a means by which certain primitive relict elements have been retained.

7. THE NATURE OF THE RACES OF *M. jurtina*

Isolating mechanisms

In spite of the widespread and largely continuous distribution of the larval foodplant of *Maniola jurtina* (*Poa* sp. and other grasses) over the greater part of its range, the insect forms very restricted populations often quite distinct from each other. *M. jurtina* is completely non-migratory, even on a local scale (Ford, 1945). Consequently, the geographical features creating isolation need not be substantial and often a short stretch

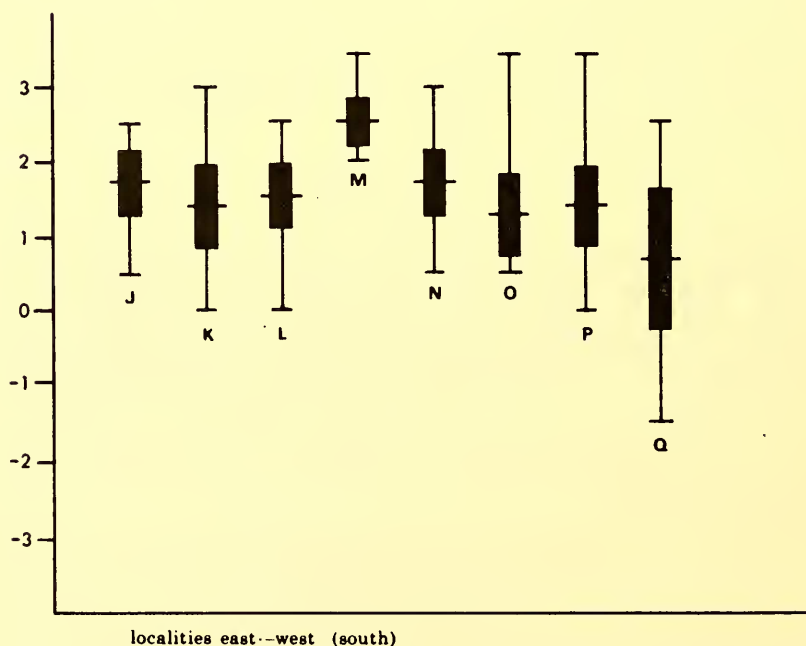
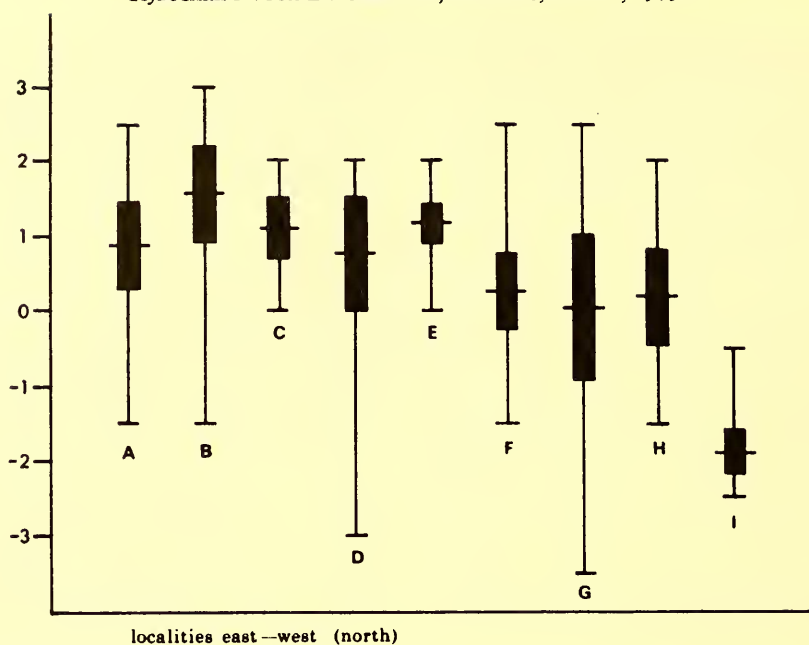


Fig. 3 and 4. Population range diagrams showing for each locality the range (thin vertical), 0.5 sd on each side of the mean (thick vertical) and the mean of F (horizontal). A. Falais, Calvados. B. Guernanville, Eure. C. Le Quesney, Seine Inférieure. D. Beauvais, Oise. E. Feucherolles, Seine et Oise. F. Chalons s/Marne, Marne. G. Chaumont en B., Haute Marne. H. Besançon, Doubs. I. Verbier, Valais. J. Santander, Spain. K. Oloron, Basses Pyrénées. L. Brassac, Tarn. M. Serignac, Gard. N. Fountain de Vaucluse. O. Digne, Basses Alpes. P. St. Valier, Alpes Maritimes. Q. Col du Tende, Alpes Maritimes

of unsuitable terrain, wide rivers or estuaries are sufficient to provide these conditions.

As has been mentioned, *jurtina* in most of its range is a low to moderate altitude insect, being local over one thousand metres and very rare over fifteen hundred. This means that the Alps and Pyrenees completely cut off the vast number of populations which exist on either side of these great mountains. It is interesting to note, therefore, that the races to the north and the south of the Alps are far less different from each other than the races to the north and the south of the Pyrenees. However, as we have seen, the Alps, Jura, Vosges and to a lesser extent the Ardennes have played a major part in creating the conditions which have produced the eastern and western type ranges.

The evolution of distinct phenotypes as a result of geographical features is to be expected where conditions permit. The discovery of sympatric evolution — that is the development of a distinct local form or race without geographical isolation — by Ford (1964) introduces a whole new dimension into the study of *jurtina* races. So far this phenomenon has not been investigated fully and it is not possible at this stage to see what effect, if any, this could have had on the evolution of *jurtina* races. However, the dimorphic females which occur in some localities might be associated with this, although to suggest such a thing is pure speculation. Sympatric evolution in this butterfly is all the more remarkable in the light of the many records of *jurtina* found copulating with other species, not only those related to it, *Pyronia tithonus* (L.) and *Aphantopus hyperanthus* (L.), but also species of a different family, *Aglais urticae* (L.), or even superfamily, *Zygaena filipendulae* (L.). It causes one to wonder what are the factors creating the sympatric situation.

It was only recently that another phenomenon was discovered in *jurtina* (Thomson, 1971 and Dennis, 1971). This I called "temporal sub-speciation" and is the occurrence of what gives all indications of being bivoltinism in what is virtually certain to be a univoltine insect (Verity, 1953). In some parts of its range, notably in the south of France, Malta and a single locality on the Isle of Wight (England) *jurtina* emerges normally and has a more or less typical flight period followed, after a break, by a "second emergence" of fresh specimens. The late individuals display quite distinctive characteristics. They are usually smaller with a smaller apical eye spot in the female and both sexes have more extensive fulvous colour, particularly in the male. Most characteristic of these *jurtina* is the considerable darkening of the underside hindwing in the female, particularly with a concurrent increase in the striae. Since publication of my paper on the discovery of this almost unique situation [it has been noted in the moth *Deuteronomos erosaria* Schiff. (Bretherton, 1955)] I have had the opportunity of examining Maltese specimens of the late emergence and these confirm what had already been observed in the Isle of Wight and south of France. The evolutionary implications of this form of temporal sub-speciation are far reaching and it deserves very close study by evolutionists.

It is likely, therefore, that *jurtina* has been subjected to two main divisions by the Alps and the Pyrenees. The form resulting from this second break could well have penetrated the south-eastern part of France, largely replacing the phenotype which existed there. Over and above the main evolutionary sub-divisions are the individual forms which have resulted from more local isolating barriers. It would be naive to assume, as some entomologists do, that the phenotypes and their distribution will remain as they are today for an indefinite or very long period of time. Such changes could occur, if not overnight, in a relatively short time in species like *jurtina*, and the unstable nature of its races and the occurrence of the phenomena which I have mentioned must be kept in mind when studying this remarkable butterfly.

Environmental effects: temperature/humidity

Two samples which I have examined from Iran perhaps give us some hint of the climatic effects on the wing markings of *jurtina*. One of these is from the hot, dry plateau just south of the main ridge of the Elburz Mountains. The other is from the more temperate and humid wooded northern watershed of that range. In the specimens from the northern region the underside hindwings of the female are very dark, with the medial band rather light whitish or silvery, the whole being covered with many dark striae. Those from the southern dry region have a very pale yellowish underside hindwing, with the medial band barely differentiated from the ground colour, except basally completely free from striae. From this it would appear that humid conditions would produce the dark striate markings, a conclusion which would concur with what is observed in the *jurtina* from north west Scotland and the Isles of Scilly. However, the variation must be genetic to a large extent, for such patterns do not prevail in maritime localities of western France or the Low Countries. A similar lack of consistency can be seen in the extent of the fulvous markings on the upperside of the butterfly throughout its range. Unjustified statements have been made that higher temperatures produce more fulvous on the wings, but this has now been proved wrong (Thomson, 1973). A high temperature, in fact, reduces the degree of fulvous on the female upperside, thus highlighting the genetic significance of the *bispulla* phenotype.

The eastern and western phenotypes

Because of the genitalia differences in the two zones which have been defined in this paper, it becomes necessary to compare the phenotypes in the east and the west. The phenetic differences, although much more marked in the south than in the north, are present on either side of the transitional zone from Sweden to the Mediterranean. Possibly the most conspicuous difference is on the underside hindwing of the female which is in the east largely free from the strongly contrasting coloration of the medial band and similarly lacking it in the medial line of the forewing. In the west these patterns frequently approach a very dark, almost blackish sepia, while in the east the predominant tones are yellowish or reddish brown. The medial band on the hindwing is much more variable in the west, but it is far less frequently of the yellowish type than in the east. The fulvous markings are so variable that only general remarks can be made. However, in the east it is usually of a much duller colour than in the west. The wing shape too is variable, but contributes towards the more robust appearance of the western form.

The east-west distribution of the valve types would at first not seem to correspond very closely to the distribution of the known phenotypes of the species. A glance at the four maps (Maps 3 - 6) would tend to substantiate this. However, if we compare the geographical races which have been named, a strong correlation can be found. In the south of France the race *miscens* Verity is quite distinct from the north Italian *phormia* Fruh. and the differences between the so-called *fortunata* of Sicily and *prae-* and *emibispulla* Verity of south Italy have been recognised for some time. In the north the position is less clear, but the mainland British race has been separated from that of Sweden. Even the transitional race of Marstrand was observed to differ from that of the east of Sweden, before it was known that this could be confirmed by an examination of the genitalia. The fact that no *bispulla*-like race has evolved to the east of Sicily, should be evidence that, at least in the south, there is a strong link between structural characters and the wing

markings. No doubt old records of "*hispulla*" in the east arose from a lack of familiarity with the south-western races of the species which differ, not only in the nature of the underside hindwing and to a lesser extent the underside forewing, but also in the extent of the fulvous.

It is obvious that the main morphological differences are in the female which makes individual correlations between this and the male genitalia rather difficult. No east-west difference has so far been detected in the female genitalia, nor is there any individual correlation between the valve and the wing patterns.

Androconia

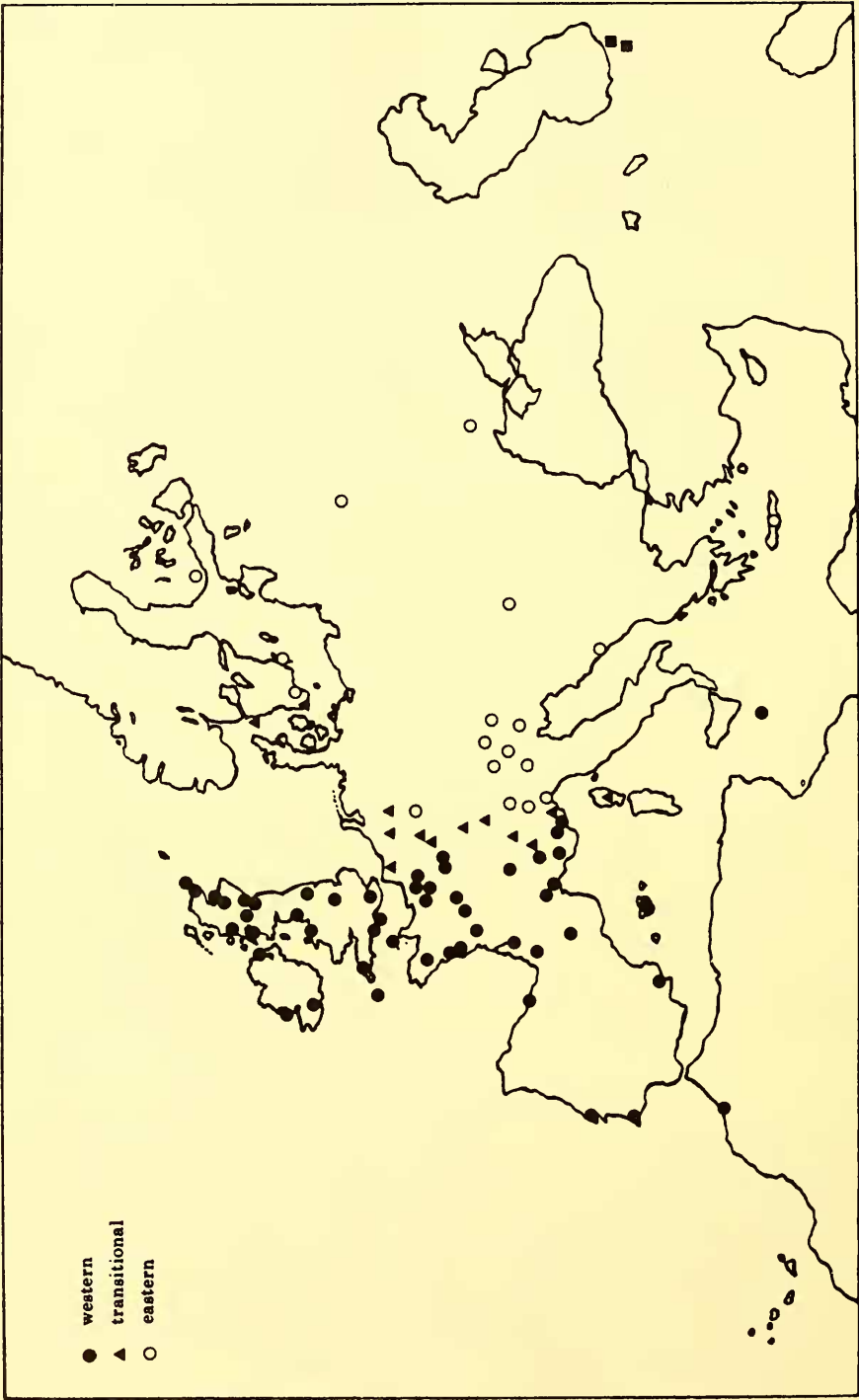
The androconial scales of *jurtina* are typical of a Satyrid being long and very narrow, tapering to almost nothing at the neck to which is attached a hair tuft. Although individually these scales vary quite a bit, extensive examination of those from different subspecies has failed to reveal any taxonomically useful character. Scales from north Africa, Crete and Iran are shown in Pl. 1 (Fig. 12-14).

On the other hand the androconial and itself is of some significance in terms of its form and variation. It has been said by some authors that *Maniola cypricola* differs from *jurtina* in that the androconial streak of the former extends beyond the third nervure, while in *jurtina* it does not (Seitz, 1908-28). Graves (1928) in his original description never claimed this, although he did comment that it was of a different shape. Even so, he acknowledged that some of the "*hispulla*" (?*fortunata*) had a similar brand. It should be noted that this is the androconial brand proper and not the dark scales which tend to extend much further. They are best detected by shining a strong light behind the specimen when the brand will show up standing out sharply as an opaque mark on a translucent ground. I have checked all of my specimens and find a most interesting situation. In the *jurtina* from Morocco and Malta the brand extends beyond the third nervure in all of the males. In Spain and Portugal the percentage with the extended brand is seventy-five (although at Santander it was zero). In the Pyrenees and Provence about a third had the brand extending beyond vein three, but this was not the case in Var and the Maritime Alps. Beyond this region and in the east the androconia never extended past the third nervure. The shape too is very variable, ranging from the broad scimitar shape described by Graves to a rather narrow and short streak in the north. In another direction it sometimes forms a rather broad blotch. Further investigations into this interesting variation would be worthwhile.

Species or subspecies

It must be considered at some point whether or not the genitalia types are indicative of distinct species. In the south where the morphological differences are so great and the border between the two zones so clear-cut, the suggestion is that the eastern and western types might well be. On the other hand in the north the morphological transition from west to east is so gradual that, with the allopatric distribution of the two types and the zone of contact being as it is, it would seem unlikely that this would be so. The genitalia variation such as is found in *jurtina* does not necessarily represent speciation: such structures are very useful diagnostically, but must never replace the true criterion for species differentiation.

The primitive type, however, poses a particular problem. Not only are the genitalia



Map. 1. The distribution of valve types in *Maniola jurtina*

differences consistent with apparently no intermediates, but the butterflies having this type of structure inhabit a rather different biotope. Unfortunately, distribution data are inadequate, but it would appear that there is an overlap between the *jurtina* populations with the primitive type valve and those with the eastern type. I am prepared to suggest that *ghilanica* could well prove to be a distinct species. This could be supported by the possible evolutionary development which I have already suggested. Certainly, other butterfly "species" have been separated on much less evidence. Until breeding and/or cytological studies or, in the case of the primitive forms, fuller distribution data prove otherwise, it is best to treat the genitalia types as representing sub-species, sub-species groups or races.

Race types and distribution

The taxonomic confusion, surrounding this species, stems mainly from the natural tendency to try to divide the species into neat and largely similar sections. This "pigeon hole" approach to the analysis of *jurtina* races soon leads to more problems than it can solve, as races and sub-species are more or less heterogeneous groups of distinct populations (Mayr, 1969). In *jurtina* this is particularly so.

The types of *jurtina* races fall into four main categories:

homogeneous — the simplest form of geographical race, but it is not found in many parts of the *jurtina* range. In isolated populations do not show consistent differences over a large area (e.g. ssp. *ghilanica*). The term "homogeneous" is used relative to the nature of the species.

clinal — in which we find a gradual change north to south or east to west or both. This is frequent not only in *jurtina* but also in other organisms (e.g. *janira*, *occidentalis*).

heterogeneous — which consists of numerous local populations, each distinct from the other, but linked by one or more main characteristics. Problems arise when the line has to be drawn between certain components of this type of race and the next, or when they are linked to adjacent races by populations consisting of both races and intermediates (e.g. *splendida*, *miscens*).

insular — in this context this type of race need not evolve on an island, but can equally well appear in an isolated continental situation. In either case the race consists of no more than a few similar populations (e.g. *cassiteridum*); insular races can be clinal, but the line of distinction is difficult to draw.

The apparent jumble of *jurtina* races with which we find ourselves, becomes much more logical when we examine the situation in the light of the material discussed throughout this paper. Indeed, the species is, in terms of geographical variation, manifestly typical. Firstly, we have the widespread race, ranging from the Baltic in the north to the Mediterranean in the south, to the Alps, Vosges and Jura in the west and to the Ural in the east. Within this race there is no more than a rather weak cline from north to south and from east to west. One part of the *jurtina* ancestor has produced a western form of the widespread race, a much more variable strain, evolving into numerous more or less distinct races. Around the perimeter of both the western and eastern widespread races has evolved the classic geographical isolate — four to the north west, possibly one or two to the south west, three to the south, at least three to the east and possibly one to the north (Map 7).

8. TAXONOMY

Although it is reasonable to suppose that in the case of *jurtina* the nature and distribu-

tion of the geographical races is now fairly well understood, taxonomic problems arise. Because of the differences in the nature of these races, it is impossible to apply uniform standards throughout. The relatively extensive areas present no problem, but a decision has to be made where the line has to be drawn between these and the individual distinct populations (demes) in one instance and the two ends of a cline in another. My judgement in respect of the recognition of races has been made bearing in mind all the relevant factors — genitalia, wing markings, presence or absence of a cline and, only in a few instances, and in connection with morphological characters, the geographical position, relative to the whole species range.

In brief, I do not believe that the taxon for a race should be adopted in the case of a single distinct population, unless this be consistently and markedly distinct in more than one single character. Nor should various grades within a cline be recognised taxonomically, unless these are clearcut sections, each quite distinct from the other, with a zone of secondary intergradation between them in some instances. In most cases even the value of recognising the forms at either end of a cline is doubtful unless the differences are considerable.

Having placed the *jurtina* races within their appropriate taxa, the question of the use of terms for infra-specific categories remains. In selecting these I have tried to be objective, but in doing so, my decisions will inevitably be criticised for both “over-splitting” and “over-lumping” simultaneously! I have tried to take the reasonable middle course. Considering the zoogeography of the *jurtina* races I do not believe that many of the described races are unjustified. The list of species group names associated with the butterfly which I have accepted as such, compares favourably with those organisms with a widespread sub-species, surrounded by distinct races at the edge of their range. The use of three categories (four, if we include the group names) provides flexibility and goes some way towards organising a species which evades attempts at categorisation. The term “race” has often been used synonymously with “subspecies”, so it is important that I define these terms in the context of this paper and in respect to the species.

sub-species: “a geographically defined aggregate of local populations which differs taxonomically from other such divisions of the species” (Mayr, loc.cit.) occupying separate and often contiguous regions.

race: a geographically defined group of populations with distinctive characters, present in most or all of the individuals but not placed in the sub-species category because —

- (a) these characters are not significantly different from other geographical races, or
- (b) the populations comprising the race represent an intermediate stage in a long cline from one sub-species to another, or
- (c) insufficient material has been examined (i.e. cited by the describer), to justify recognition as a sub-species.

form: a potential race or sub-species, but not classified as such, because no justification for taxonomic separation has at this time been found, or a population (or group of populations) which has been described as a distinct race or sub-species, but which in my opinion is synonymous with a previously described race or sub-species, or barely distinct from it.

In the following account I have avoided irrelevant synonymy and the repetition of adequate descriptions which can be found elsewhere. Only a reference to the literature in which this can be found is given. However, where no description in detail has been made, or where the original description or subsequent descriptions are misleading, a redescription

has been made. This takes the form of a fairly general description of the main features of both sexes, followed by a statement of the variation trends. The average wingspan and that of the smallest and largest specimen is given as twice the distance from the centre of the thorax to the apex of the forewing. In the male the ground colour of fresh examples varies little throughout the range of the species. It is, when freshly emerged, a very dark brown-sepia, almost black basally. No mention is thus made of this character. In the female this varies from dark brown-sepia, though not as dark as the male, to a rather greyish brown-sepia. The first colour form I have referred to as "dark" and the second "light".

I have included an alphabetical list of all names associated with *jurtina*, including those which are infra-subspecific. The names coined by Leeds (1950), are excluded, unless these are known forms of the species and not hypothetical concepts or synonyms. The full bibliographic references to all but one of these names can be found in this or previous papers (Thomson, 1969 and 1970). The one omission is *anticoextensa* Leeds (*loc.cit.*, p. 106) which was inadvertently left out of my original list and is the form in which the apical eyespot of the forewings is elongated (but not downwards).

MANIOLA Schrank, 1801: 152, 170

Type: *jurtina*

GENITALIA WESTERN OR TRANSITIONAL

jurtina - group

Maniola jurtina jurtina (Linnaeus)

Papilio jurtina Linnaeus, 1758: 124.

Type locality. Europe and Africa — Linnaeus, 1758. North Africa — Verity, 1913: 184—185.

Genitalia: western (illustrated by Le Cerf, 1913)

Description. Male — 58.3 mm (smallest 54.0: largest 62.0); upperside: forewing fulvous scaling orange, suffuse and variable. Apical eyespot moderately large, rather diffuse but distinctly pupilled. Androconial band well defined, extending beyond vein three. Hindwing without fulvous scaling; underside: forewing basal and discal areas light reddish fulvous slightly darker than the submarginal, band with a distinct medial line. Outer margin and termen greyish, inwardly edged with dark grey-brown, lightly striate. Apical eyespot moderately large, usually single pupilled. Hindwing basal and discal areas and outer margin light greyish brown. Medial band greyish usually with three or four ocelli unpupilled and encircled with fulvous, wing lightly striate.

Female — 61.2 mm (smallest 60.0: largest 63.0); upperside: forewing fulvous scaling orange extending well into the discal area. Submarginal band extensive, strongly broken by the ground colour along the nervures. Apical eyespot large, usually bipupilled. Hindwing with submarginal fulvous band; underside: forewing basal and discal areas light reddish fulvous contrasting with the light fulvous submarginal band with a very dark medial line. Outer margin and termen greyish, inwardly edged with dark grey-brown, striate. Apical eyespot large, often bipupilled. Hindwing basal and discal areas and outer margin greyish or greyish fulvous. Medial band greyish, usually without ocelli and inwardly edged with a line of suffuse light fulvous, wing striate.

Variation consists mainly in the extension of the fulvous in the male which sometimes forms an indistinct band mixed with the ground colour. In the female the forewing discal fulvous can be more or less mixed with the ground colour and the submarginal band more or less broken by the nervures. The female underside hindwing varies towards a yellowish fulvous or light violet grey.

Diagnostic. The large size, the long androconial and in the male and submarginal band of the female upperside forewing broken by the nervures are distinctive features.

Range. Algeria, Tunisia and Morocco. Canary Islands as *f. fortunata*.

Discussion. The question of deciding upon the typical sub-species is certainly not free from controversy and largely depends on one's interpretation of who was the "first reviser" in respect of restricting the type locality. Lempke (1935: 182) was of the view that Linnaeus himself was instrumental in restricting the type locality to Sweden because the first mention of the species in a restricted locality was in Fauna Svecica (1761: 276). However, I would tend to agree with Mayr (1969: 403) that

"... in order to qualify as first reviser an author must give evidence of a choice between available alternatives". Verity was there the author who took the adequate action in restricting the type locality to north Africa (see Hemming, 1968: 185) even although I would not necessarily agree that his basis for doing so (the origin of the Linnean "type") was correct (Thomson, 1971: 92).

form *fortunata* Alphéraky

Epinephele janira var. *fortunata* Alphéraky, 1889: 222, pl. 11, fig. 4.

Type locality. Orotava, Teneriffe, Canary Islands - Alphéraky, 1889.

Genitalia. Western.

Description and diagnostic. The form *fortunata* appears to differ from *jurtina* from north Africa only in its slightly larger size, slightly darker ground colour and more concave costa of the female forewing. A recently received sample from Teneriffe were of a form with female underside markings much closer to the race from Malta than I have seen, although the uppersides retained the characters associated with *fortunata*. I suspect that these were exceptional.

Range. Canary Islands.

Discussion. Unfortunately I do not have sufficient material to determine whether or not there are significant differences between this form and the typical sub-species.

Maniola jurtina hyperhispulla subsp. nov.

Holotype. Male - Buskett, Malta. May 1971 (Anthony Valletta).

Paratypes. 2 males - "Malta, 1969", 1 female - Buskett, Malta. 3 September 1971 (Anthony Valletta). Holotype and paratypes in the author's collection.

Genitalia. Western.

Description. Form A (early).

Male - 55.1 mm (smallest 52.0; largest 58.0); upperside: forewing fulvous scaling orange forming a distinct band. Apical eyespot moderately large, well defined, distinctly pupilled. Androconial band well defined usually extending beyond vein 3. Hindwing without fulvous scaling; underside: forewing basal and discal areas light reddish fulvous, slightly darker than the submarginal band with an indistinct medial line. Outer margin

and termen greyish, inwardly edged with dark brown, lightly striate. Apical eyespot moderately large, usually single pupilled, surrounded by light fulvous. Hindwing basal and discal areas and outer margin greyish brown, medial band greyish, usually with three or four ocelli unpupilled and encircled by fulvous. Wing lightly striate.

Female - 57.6 mm (smallest 53.0: largest 60.0); upperside: forewing fulvous scaling orange, largely covering the discal and basal areas. Submarginal band extensive, not separated from the discal fulvous, nor broken by the ground colour along the nervures. Apical eyespot large, usually pupilled. Hindwing with a submarginal fulvous band occasionally extending basally; underside: forewing basal and discal areas light reddish fulvous contrasting with the lighter submarginal band, with a distinct medial line. Outer margin and termen light greyish or light yellowish grey, inwardly edged by dark brown, striate. Apical eyespot large, often bipupilled. Hindwing basal and discal areas and outer margin grey brown. Medial band greyish or silvery usually without ocelli, inwardly edged with a very distinct band of bright fulvous.

Variation consists of the lightening or darkening of the underside hindwing in the female, giving the effect of greater or lesser contrast with the medial band.

Form B (late).

Male - none available for study.

Female - 57.9 mm (smallest 54.0: largest 60.0); upperside: forewing fulvous scaling orange, extending well into and occasionally largely covering the discal and basal areas. Submarginal band extensive, not broken by the ground colour along the nervures. Apical eyespot large, usually bipupilled. Hindwing with a submarginal fulvous band occasionally extending basally; underside: forewing basal and discal areas light reddish fulvous contrasting with the fulvous of the lighter submarginal band with a distinct medial line. Outer margin and termen dark greyish fulvous strongly striate and inwardly edged with dark grey brown. Apical eyespot large and often bipupilled. Hindwing basal and discal areas and outer margin dark greyish fulvous. Medial band greyish fulvous with no, one, or two ocelli, occasionally pupilled and encircled with fulvous, inwardly edged by a very indistinct fulvous suffusion. Wing strongly striate.

Variation consists mainly in the extent of fulvous in the discal area of the upperside forewing and the enlargement of the apical eyespot.

Diagnostic. By the extent of fulvous in both sexes and the conspicuous fulvous edging of the female underside hindwing medial band, this sub-species differs from *M. jurtina jurtina* and *M. jurtina hispulla*, although the smaller *hispulla* male occasionally has a bright submarginal fulvous suffusion on the upperside forewing.

Range. Known only from Malta.

Discussion. The differences between the early and late forms are interesting. The later specimens are rather more variable than the early ones. It is unfortunate that late males were not available for comparison.

Maniola jurtina hispulla Esper

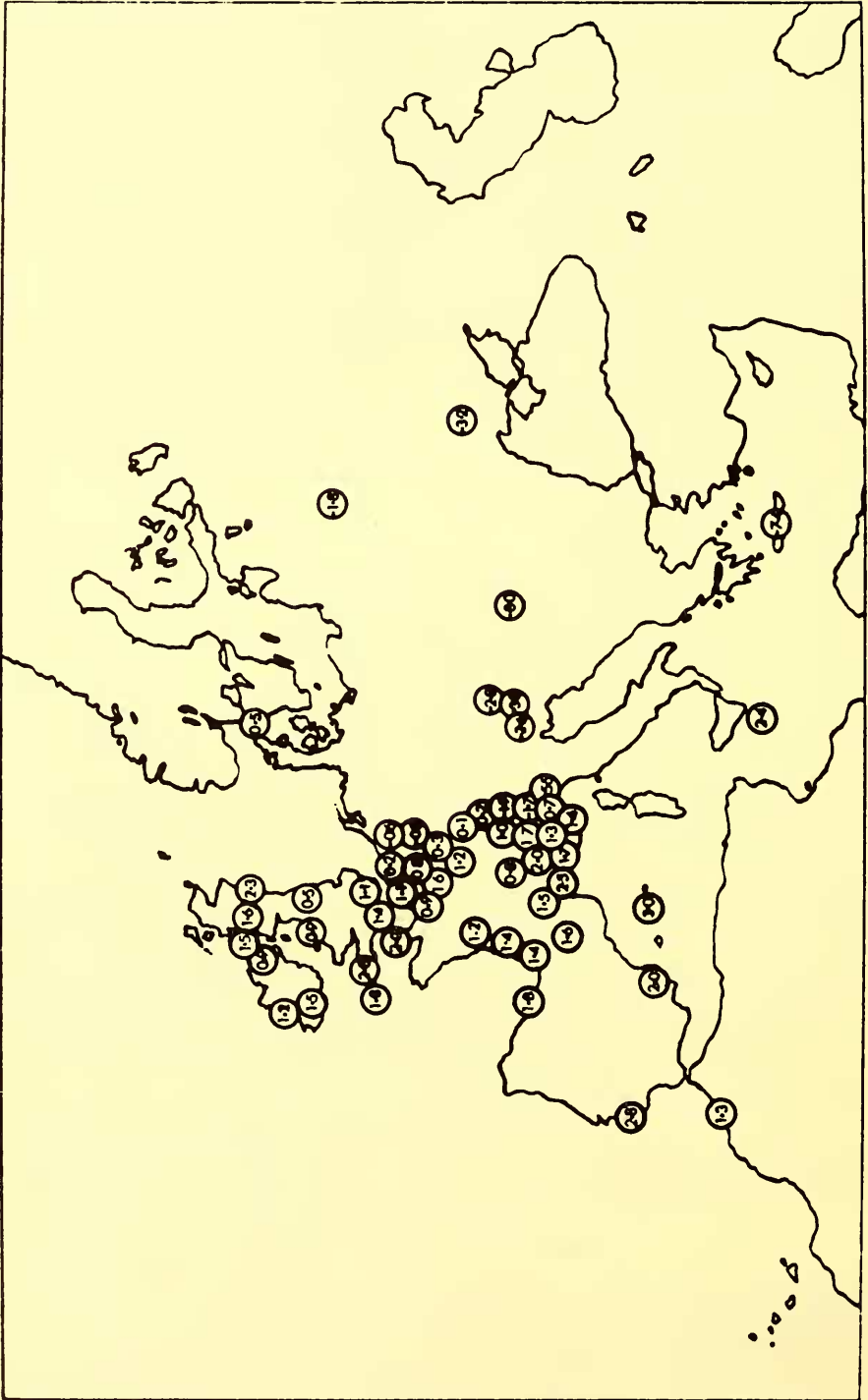
Papilio Hispulla Esper, 1805: II, pl. CXIX.

Papilio Hispulla Hübner, 1805: 27, figs. 593—596.

Type locality. Lisbon - Esper, 1805.

Genitalia. Western.

Description. Male - 52.0 mm (smallest 48.0; largest 58.0); upperside: forewing



Map. 2. The distribution of the value of F in *Maniola jurtina*

fulvous scaling orange suffuse and variable. Apical eyespot rather small, but sometimes moderately large, diffuse, indistinctly pupilled. Androconial brand well defined frequently extending beyond vein 3. Hindwing without fulvous scaling; underside: forewing basal and discal areas light yellowish or reddish fulvous, barely distinguishable from the submarginal band with an indistinct medial line. Outer margin and termen greyish or greyish brown almost without striae. Apical eyespot usually rather small, usually single pupilled, surrounded by light fulvous. Hindwing basal and discal areas and outer margin greyish or greyish brown. Medial band usually lighter, with two to four ocelli, unpupilled and encircled with fulvous. Wing almost without striae.

Female — 54.7 mm (smallest 52.0; largest 58.0); upperside, forewing fulvous scaling orange, extending well into the discal area. Submarginal band extensive occasionally broken by the ground colour along the nervures. Apical eyespot large usually bipupilled. Hindwing nearly always with a submarginal fulvous band; underside: forewing basal and discal areas reddish fulvous, contrasting strongly with the lighter submarginal band, with a distinct medial line. Outer margin and termen greyish or dark greyish yellow, darker inwardly, lightly striate. Apical eyespot large, often bipupilled surrounded by light fulvous. Hindwing basal and discal areas and outer margin greyish brown or dark greyish yellow. Medial band light greyish or greyish yellow, usually suffused with more or less distinct fulvous, usually with 0—2 unpupilled ocelli, encircled with fulvous. Wing lightly striate.

Diagnostic. Differs from *jurtina* in its much smaller size and less constant fulvous markings and from *hyperhispulla* in its smaller size and much less bright female underside.

Range. Spain and south-east France, north of the Cantabrian Mountains as race *cantabrica* and in south-east France as race *miscens*, the Balearic Islands and probably also Sardinia.

Discussion. The Spanish *hispulla* is an extremely variable creature and some populations—in northern and upland areas of the Iberian Peninsula would probably be applicable to *cantabrica* or *miscens*. More work is necessary on the species in central Spain.

race *cantabrica* Agenjo

Epinephele jurtina cantabrica Agenjo, 1934: 313.

Type locality. Camargo, Santander, Spain — Agenjo, 1934.

Genitalia. Western. Rarely a relict transitional type occurs.

Description. Agenjo, 1934. Male — 51.0 mm (smallest 50.0; largest 52.0); upperside: forewing fulvous scaling suffuse and variable. Apical eyespot moderately large, rather diffuse and distinctly pupilled. Androconial brand fairly well defined, not extending beyond vein three. Hindwing without fulvous scaling; underside: forewing basal and discal areas reddish fulvous, contrasting with the lighter submarginal band, with a distinct medial line. Outer margin and termen greyish brown lightly striate, darker inwardly. Apical eyespot rather large, usually single pupilled, but not infrequently unpupilled. Hindwing basal and discal areas and outer margin greyish brown. Medial band lighter with two to three ocelli, unpupilled and encircled with fulvous. Wings lightly striate;

Female — 56.2 mm (smallest 51.0; largest 58.0); upperside: fulvous scaling orange, present as a suffuse patch in the discal area. Submarginal band well developed, frequently broken by the ground colour along the nervures. Apical eyespot usually bipupilled. Hind-

wings with occasional submarginal fulvous; underside: forewing basal and discal areas reddish fulvous, contrasting with the lighter submarginal band with a distinct medial line. Outer margin and termen greyish brown or brown rather heavily striate. Apical eyespot large often bipupilled. Hindwing basal and discal areas and outer margin dark yellowish grey or brown. Medial band greyish yellow or greyish fulvous usually with 0—2 ocelli. Wing rather strongly striate.

Variation is principally in the size of the apical eyespot, the greater or lesser encroachment of the ground colour into the fulvous areas and the coloration of the underside hindwing in the female.

Diagnostic. Differs from *hispulla* in the indistinct discal and hindwing, fulvous of the female upperside and the dark underside forewing, fulvous in the two sexes.

Range. Spain north of the Cantabrian Mountains.

Discussion. The number of individuals which fly with *cantabrica* but which are to all intents and purposes indistinguishable from *hispulla*, varies from year to year, occasionally forming a very large minority of the population.

race *miscens* Verity

Maniola jurtina race *miscens* Verity, 1953: 268.

Type locality. St. Barnabé, Nice, Alpes Maritimes — Verity, 1953.

Genitalia. Western with (rarely) relict transitional types.

Description. Male — 52.4 mm (smallest 46.0: largest 59.0); upperside: forewing fulvous scaling orange, occasionally yellowish suffuse and variable occasionally forming a band below the apical eyespot or extending basally. Apical eyespot moderately large distinctly pupilled with white. Androconial brand fairly well defined rarely extending beyond vein three; underside: forewing basal and discal areas light fulvous, barely distinguishable from the submarginal band, with no medial line. Outer margin and termen greyish, usually almost without striae. Apical eyespot moderately large, usually single pupilled. Hindwing basal and discal areas and outer margin greyish or light greyish-brown, medial band a little lighter, usually with two to four ocelli, encircled with fulvous. Wing almost without striae; female — 56.7 mm (smallest 50.0: largest 61.0); upperside: forewing fulvous scaling orange, occasionally yellowish, present as a suffuse patch or extending well into the discal area. Submarginal band well developed, occasionally broken by the ground colour along the nervures. Apical eyespot moderately large, sometimes bipupilled. Hindwing almost always with a submarginal fulvous or light or extensive suffusion; underside: forewing basal and discal areas light fulvous or light reddish fulvous, slightly darker than the submarginal band, with a distinct medial line. Outer margin and termen greyish, light greyish brown or greyish yellow, lightly striate. Apical eyespot moderately large, often bipupilled. Hindwing basal and discal areas and outer margin greyish, light greyish brown or greyish yellow. Medial band light greyish or greyish yellow, often without ocelli. Wing lightly striate.

Variation is in the extent of the fulvous and the size of the apical eyespot in both sexes, although only rarely does the female upperside marking approach that of *ssp. occidentalis*.

Diagnostic. Differs from *hispulla* in the colour of the underside hindwing of the female and in being generally less brightly and more inconsistently marked with fulvous.

Range. South-east France in the Department of Alpes Maritimes, Var, Basses Alpes,

Hautes Alpes, Bouches du Rhône, Vaucluse, Drôme, Gard and possibly also Ardèche, Hérault, Aude and Pyrénées Orientales.

mirtyllus-group

Maniola jurtina mirtyllus Fourcroy

Papilio mirtyllus Fourcroy, 1785: 239.

Type locality. Not specified. Fourcroy's description appeared in a work on the Lepidoptera of the Paris region. It is best, therefore, to consider the type locality of the ssp. *mirtyllus* as north-east France.

Genitalia. Transitional with both western and (in the eastern part of its range) eastern types.

Description. Male — 46.8 mm (smallest 43.0: largest 50.0); upperside: forewing fulvous scaling orange suffuse and variable. Apical eyespot rather small, diffuse, indistinctly pupilled. Androconial brand suffuse, not extending beyond vein three. Hindwing without fulvous; underside: forewing basal and discal areas light fulvous, barely darker than the submarginal band, without medial line. Outer margin and termen greyish, without striae. Apical eyespot rather small, usually single pupilled. Hindwing basal and discal areas and outer margin greyish. Medial band slightly lighter, usually with two or three ocelli, unpupilled and encircled with fulvous. Wing lightly striate; female — 51.7 mm (smallest 45.0: largest 57.0); upperside: forewing fulvous, scaling yellowish or orange, present as a suffuse patch in the discal area. Submarginal band well developed, not broken by the ground colour along the nervures. Apical eyespot moderately large, usually single pupilled. Hindwing usually without fulvous; underside: forewing basal and discal areas light reddish fulvous, barely contrasting with the lighter submarginal band, with a distinct medial line. Outer margin and termen yellowish grey or greyish brown, lightly striate. Apical eyespot moderately large, usually single pupilled. Hindwing basal and discal areas and outer margin yellowish grey or greyish brown. Medial band light yellowish grey or greyish, usually without ocelli. Wing lightly striate; variation is usually in the female upperside forewing fulvous which is also occasionally present in the building. The apical eyespot in both sexes varies a lot in size.

Diagnostic. In addition to the genitalia this sub-species differs from *insularis* in the more uniform underside of both sexes by the usual lack of the medial line on the underside forewing of the male and from *miscens* in its smaller size and less extensive female fulvous.

Range. South west Sweden, (Norway), Denmark, Netherlands, Belgium and France, roughly north and east of a line from Pas de Calais to the Franco-Italian border. See map 1 for distribution of genitalia types.

Discussion. The ssp. *mirtyllus* form a north to south cline, the limits of which are very different from each other. In the north the small dark race from southwest Sweden blends into the comparatively constant central form which is found in the Low Countries and most of northeast France. At its southern end we find a singularly large race with rather extensive fulvous in some parts of Haute Savoie. The dimensions given are for the central part of the cline (Belgium). The figures for populations to the north and south are:

southwest Sweden	— male	45.0 mm (smallest 39.0: largest 50.0)
	female	47.6 mm (smallest 44.0: largest 52.0)
Hautes Savoie	— male	49.0 mm (smallest 46.0: largest 51.0)
	female	53.8 mm (smallest 52.0: largest 58.0)

Some transitional populations in the Alpes Maritimes (e.g. Col du Tende) are probably more applicable to ssp. *emibispulla*.

Maniola jurtina occidentalis Pionneau

Epinephele janira ab. *occidentalis* Pionneau, 1924: 58.

Epinephele janira ab. *meridionalis* Pionneau, 1924: 58.

Type locality. West France — Pionneau, 1924.

Genitalia. Western, with the occasional relict transitional type.

Description. Male — 50.1 mm (smallest 46.0: largest 55.0); upperside: forewing fulvous scaling orange, suffuse and variable, but usually confined to a ring around the eyespot. Apical eyespot rather small, diffuse and indistinctly pupilled. Androconial brand suffuse, not extending beyond vein three. Hindwing without fulvous; underside: forewing basal and discal areas fulvous or light fulvous, barely darker than the submarginal band, usually with no medial line. Outer margin and termen greybrown, lightly striate. Apical eyespot rather small, usually single pupilled. Hindwing basal and discal areas and outer margin grey-brown. Medial band slightly lighter, usually with two or three ocelli, unpupilled and encircled with fulvous. Female — 54.5 mm (smallest 50.0: largest 60.0); upperside: fulvous scaling yellowish or orange present as a suffuse patch in the discal area. Submarginal band usually well defined, frequently broken by the ground colour along the nervures. Apical eyespot moderately large, often bipupilled. Hindwing usually with a submarginal fulvous suffusion or "point"; underside: forewing basal and discal areas reddish fulvous, dark fulvous or fulvous, darker than the submarginal band usually with a distinct or rather dark medial line. Outer margin and termen light greyish, dark greyish-brown or dark yellowish fulvous moderately, or rather heavily striate. Hindwing basal and discal areas and outer margin greyish brown, dark grey-brown, or dark yellowish fulvous. Medial band greyish, light greyish or yellowish with 0—2 ocelli unpupilled. Wing moderately or rather heavily striate.

Variation is in the female upperside forewing submarginal fulvous band and in the fulvous of the hindwing which is more or less extensive. The various colour forms of the female underside hindwing are confusing, tending towards a rather monochrome grey on the one hand to a fairly bright yellow fulvous on the other.

Diagnostic. Differs from *miscens* in its smaller size and considerably less extensive fulvous in the female, also by the smaller and more suffuse apical eyespot of the male.

Range. France south and west of the range of ssp. *mirtyllus* and north and west of the range of race *miscens*.

Discussion. Pionneau wrote of var. *meridionalis* (1936): "Dans le Sud-Ouest de la France, en Gironde, on ne rencontre pour ainsi dire que cette race."

Also his original description of "ab. *meridionalis*" is decidedly vague: "... qui est d'une manière générale d'un brun très foncé dans le midi de la France."

One cannot draw any useful conclusion from such a misleading description. I have examined a number of representative series from Gironde, Dordogne and Loire Inferieure

and find that there is no justification for separating them as a distinct race — nor even for recognising Pionneau's *meridionalis* as a form.

The northeastern region in which this sub-species merges with *mirtyllus* is complex. The characters of *occidentalis* may be found in populations with transitional type genitalia and those of *mirtyllus* with western type genitalia.

splendida-group

***Maniola jurtina splendida* Buchanan White**

Epinephele janira var. *splendida* Buchanan White, 1871: 200.

The locality. Longa Island, Ross-shire, Scotland — Buchanan White, 1871.

Genitalia. Western.

Description. Graves, 1930: 50. Thomson, 1969: 56—57 (includes a distribution map). Thomson, 1970: 261—268.

For the range of variation in this race, see Thomson, 1970 (l.c.) in which will be found an account of the various forms which the sub-species takes.

Diagnostic. Best distinguished by the very dark underside (particularly the hindwing) of the male, the dark striate ground colour of the underside hindwing of the female, with "Hübner's mark" present in most individuals; also by the extensive and rather dark fulvous of both sexes.

Range. Throughout the Western Isles, on Orkney, northwest Scotland to south of the Caledonian Canal forming a cline further south and east with ssp. *insularis* in which both sub-species and intermediates are found.

Discussion. Buchanan White's original description mentions that he had seen specimens of "var. *splendida*" from Nice. What he had seen, would probably have been *miscens*, an example of which still exists in his depleted collection, housed in the Perth County Museum.

***Maniola jurtina cassiteridum* Graves**

Maniola jurtina cassiteridum Graves, 1930: 75, pl. 1, fig. 7, 8, 9.

Type locality. Isles of Scilly (England) — Graves, 1930.

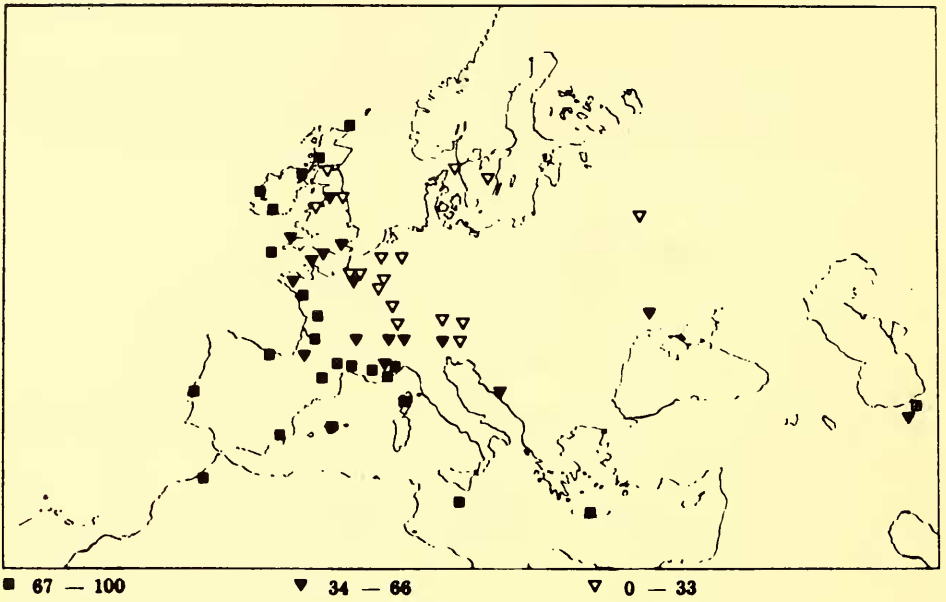
Genitalia. Western.

Description. Graves, 1930.

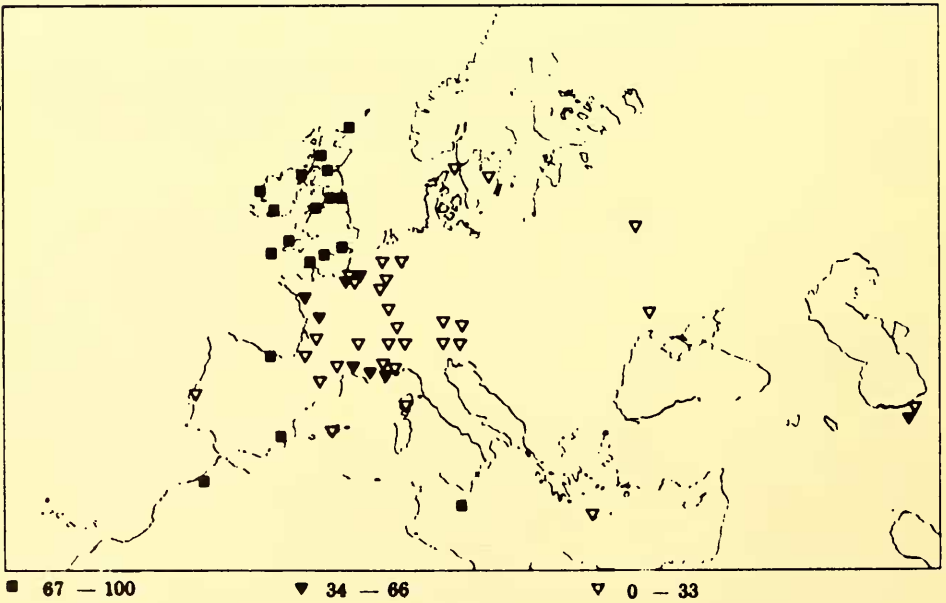
Diagnostic. The most distinctive feature of this race is the remarkable underside of the female hindwing which has the heavy striae and strongly contrasting light medial band. This is also a feature of the male but this sex is more easily distinguished by the large, often white pupilled, orange ringed ocelli on the underside hindwing.

Range. The Isles of Scilly and (with characters less pronounced) Lundy Island and Alderney (Channel Islands).

Discussion. A remarkable and probably significant fact is that the late *jurtina* on the Isle of Wight (see page 14) resembles this race to some extent on the underside of both sexes. Furthermore, *cassiteridum* is on the wing (sometimes fresh) throughout September, when the *jurtina* on the adjacent Cornish Peninsula are over, or almost so. Some of the females on Lundy Island tend towards the Irish *iernes*.

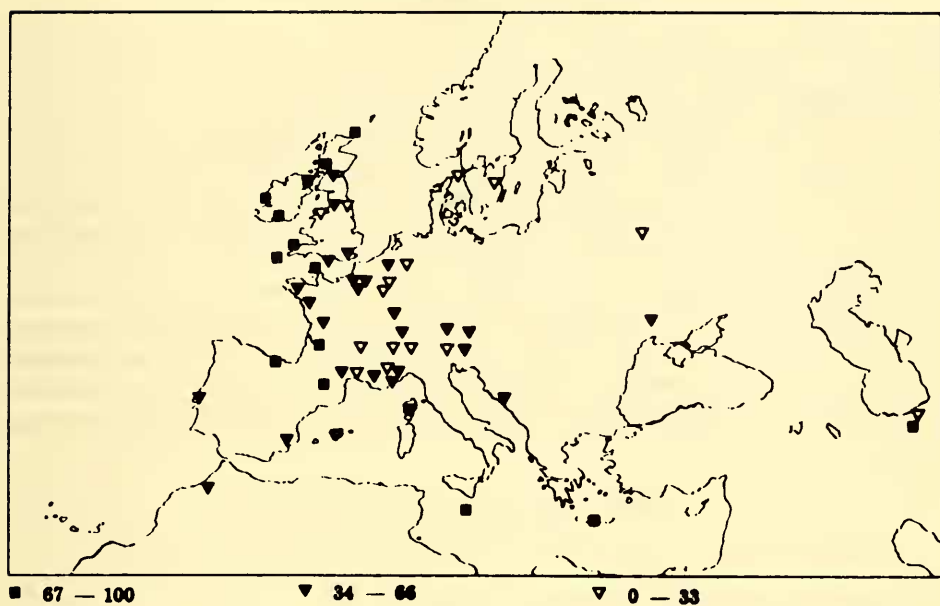


Map 3

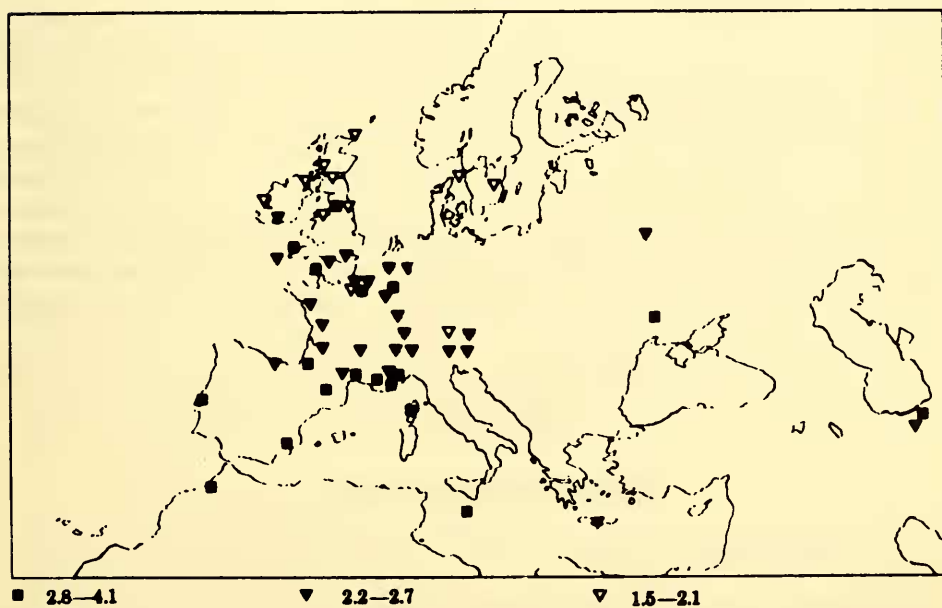


Map 4

Maps 3—6. The distribution of morphological characters in *Maniola jurtina*. 1. females with fulvous on the upperside hindwing; 2. males with a medial line on the underside forewing; 3. females with the apical eyespot bipupilled on either surface; 4. male average spotting on the underside hindwing



Map 5



Map 6

***Maniola jurtina iernes* Graves**

Maniola jurtina iernes Graves, 1930.

Type locality. Co. Kerry, Eire (Ireland) — Graves, 1930.

Genitalia. Western with the very occasional relict transitional type structure.

Description. Graves, 1930.

Diagnostic. The very large gynaikotropic males, with extensive fulvous markings and even larger females, with brilliantly coloured undersides, are easily distinguished from any other race.

Range. Ireland, with characters less distinct in parts of the north, Isle of Man.

Discussion. In the north of Ireland (e.g. Coleraine) a percentage of the females are virtually indistinguishable from bright maritime *insularis* and some rather diminutive males also turn up. The race on the Isle of Man agrees in every respect with *iermes* from southern Ireland, except that it is considerably smaller, 45.2 mm in the male and 48.9 mm in the female (see Thomson, 1971).

***Maniola jurtina insularis* Thomson**

Maniola jurtina insularis Thomson, 1969: 53—55, pl. 1, fig. 1—4, 6—8, 11—12.

Type locality. Isle of Wight, England — Thomson, 1969.

Genitalia. Western, with the very occasional relict transitional type.

Description. Thomson, 1969. (*loc.cit.*)

Diagnostic. The contrasting underside forewing of the male, with the well marked dark medial line, is distinctive, as is the bright contrasting underside of the female. The fulvous is generally fairly extensive in the female — particularly on the forewing.

Range. England, Wales, Scotland to the Clyde in the west and Aberdeen in the east forming a cline further north and west with ssp. *splendida* in which both sub-species are found with intermediates.

Discussion. The mainland British *insularis* is a remarkably heterogeneous sub-species with populations of adjacent localities, consisting of quite different phenotypes. A close approach to ssp. *mirtyllus* can be found in some localities in Surrey and there are localities in North Wales in which the characteristics of the race are not well developed.

GENITALIA EASTERN*janira* - group***Maniola jurtina janira* Linnaeus**

Papilio janira Linnaeus, 1758: 475.

Papilio monoculus Goeze, 1779: 285.

Type locality. Europe — Linnaeus, 1758. Central Europe — Verity, 1913: 184—185. Because of the differences in the genitalia the restriction of the type locality by Verity is inadequate. Action is necessary, to avoid confusion between the type locality of *janira* (ssp. of *jurtina* L.) and the western sub-species *mirtyllus* and *occidentalis*. SOUTH GERMANY is therefore made the new restricted type locality of the sub-species *janira*.

Genitalia. Eastern.

Description. Male — 48.2 mm (smallest 44.0; largest 55.0); upperside: forewing fulvous orange, confined to a ring around the eyespot. Apical eyespot rather small, diffuse, indistinctly pupilled. Androconial band suffuse, not extending beyond vein three. Underside: forewing basal and discal areas light reddish fulvous, barely distinguishable from the submarginal band with no medial line. Outer margin and termen greyish or greyish brown without striae. Apical eyespot rather small, usually single pupilled, sometimes surrounded by light fulvous. Hindwing basal and discal area and outer margin greyish or greyish brown. Medial band slightly lighter usually with two or three ocelli, unpupilled and encircled with fulvous. Wing very lightly striate. Female — 51.4 mm (smallest 47.0; largest 56.0); upperside: forewing fulvous scaling yellowish or orange present as a suffuse patch in the discal area. Submarginal band very variable, fairly well defined, occasionally broken by the ground colour along the nervures. Apical eyespot moderately large usually single pupilled. Hindwing usually without fulvous; underside: forewing basal and discal areas light reddish fulvous slightly darker than the submarginal band usually with an indistinct medial line. Outer margin and termen yellowish grey or greyish brown lightly striate. Apical eyespot moderately large usually single pupilled but not infrequently bipupilled. Hindwing basal and discal areas and outer margin yellowish grey or greyish brown. Medial band light yellowish grey or greyish usually without ocelli. Wing lightly striate.

Variation is considerable in the extent and form of the female upperside fulvous markings, but they rarely approach that of the races found further south. The apical eyespot can be rather large or small.

Diagnostic. Differs from all other eastern races by the small size and inextensive fulvous of the female upperside.

Range. Finland, northeast U.S.S.R., Germany, Switzerland, Austria and the far north of Italy, and eastwards probably as far as Czechoslovakia and Hungary. Further south it is found as the races *phormia* and *praehipulla*, further eastward as the race *strandiana* and possibly also *megala* and *maraschi*.

Discussion. The eastern and south eastern limits of *janira* are not well known, particularly in its transition to *strandiana* and in Turkey, where it possibly flies with *telmessia*. I have not included southwest Sweden within the range of the sub-species. The specimens I have with eastern genitalia from that region differ markedly from the widespread *janira* in their small size, very pale female underside and blind apical eyespot on the upperside of both sexes. Unfortunately I do not have sufficient material on which to base a fuller description, but these specimens will probably represent another case of a *jurtina* race, developing at the edge of the species range.

race *megala* Oberthür

Epinephele janira race *megala* Oberthür, 1909: 387.

Type locality. Akbès — Oberthür, 1909.

Genitalia. Two specimens dissected by Bernardi were thought to be of the eastern type *a* but the work of Tauber (1970) indicates that these and others found since in southern Turkey were of a quite distinct type. Examination of the Turkish populations using adequate sampling techniques is essential before conclusions can be made regarding the situation in this area.

Description. Oberthür's original description reads:

"... La plus grande forme géographique de *janira* que je connaisse est celle d'Akbès. Elle est plus grande que *fortunata*, Alphéraký ... Outre sa taille, elle se distingue par la profonde dentelure de ses ailes inférieures, par le coloris gris ou jaune brun du dessous des ailes inférieures qui, chez la ♀, est généralement assez sombre, c'est-à-dire très peu coloré de jaune en dessus et aussi par le développement de la tache noire subapicale ocellée, aux ailes supérieures. Je possède 7 ♂ et 9 ♀; un des ♂ a 5 taches noires cerclées de jaune, dont 4 pupillées de blanc, sur les ailes inférieures, en dessous. Il lui manque le 3e ocelle pour équivaloir au n° 429 d'Herrich-Schaeffer, mentionné ci-dessus, et dont la localité m'est restée inconnue. J'ai donné à la belle race géographique d'Akbès le nom *megala* ..."

Diagnostic. Presumably the very large size of this race should identify it.

Range. Akbès and according to Graves (1933: 179) Shar Dewesy on the Turco-Syrian borderland and Marmarice.

Discussion. Material was not available to supplement Oberthür's rather inadequate description.

form *antalyana* Tauber

Maniola megala antalyana Tauber, 1970: 109—111.

Type locality. Bay Dagliari, Yazir westl. Antalya, c. 1000 m — Tauber, 1970.

Genitalia. Of the type called "*megala*" by Tauber.

Description. Tauber, 1970.

Range. So far only in the type locality.

Discussion. Described as a subspecies of "the species *megala*" this form representing a single population in a remote part of Turkey and described from a very small sample must be studied more fully before being recognised as a subspecies or even a race.

race *maraschi* Pfeiffer

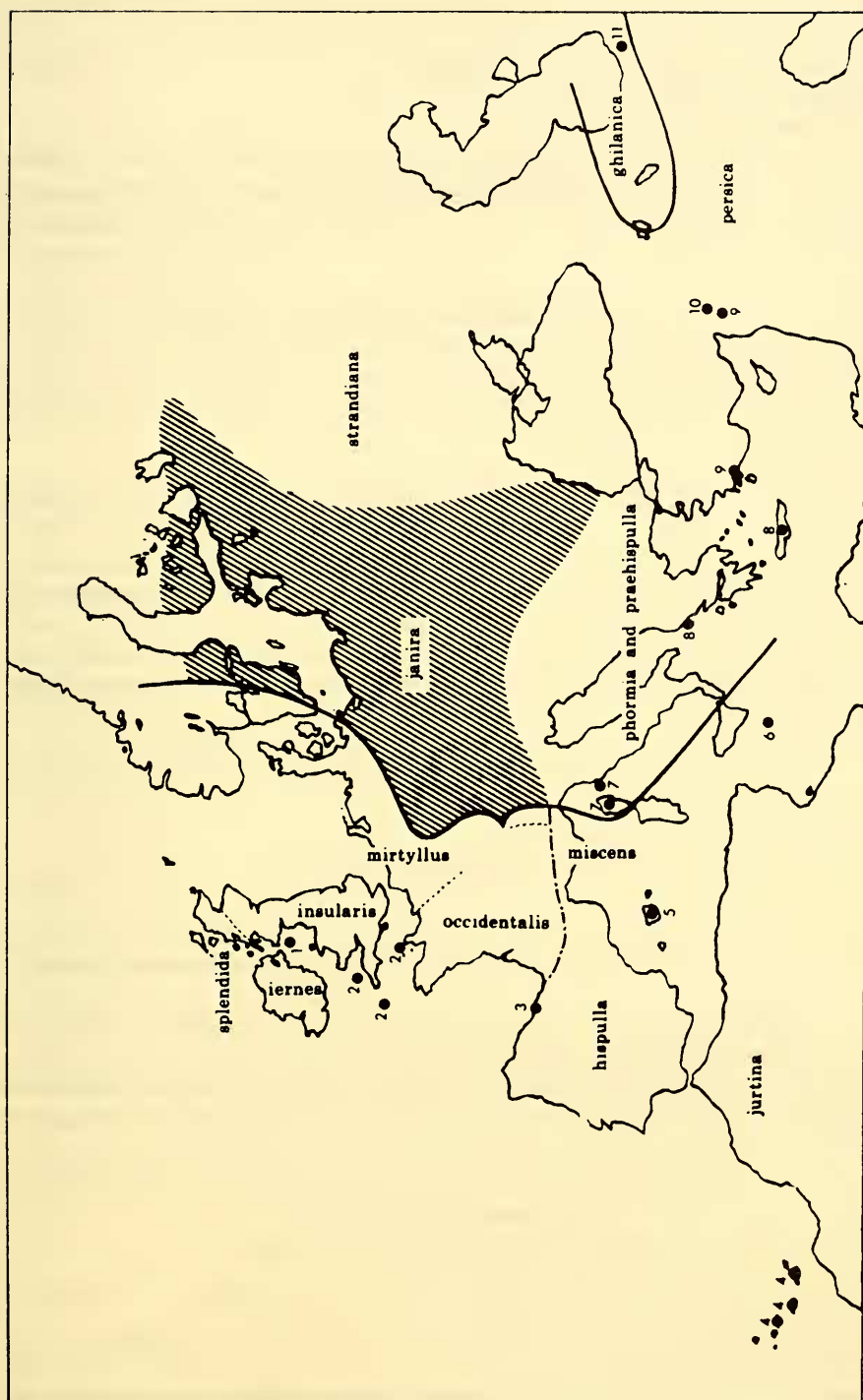
Epinephele jurtina maraschi Pfeiffer, 1932: 24.

Type locality. Marasch — Pfeiffer, 1932.

Genitalia. Tauber (1970) found the "*megala*-type" in this race but further study is required.

Description. Pfeiffer's original description reads:

"... Die Art dürfte hier ihre Südgrenze in einer grossen, auffallend breitflügeligen Rasse erreichen. Das ♂ gleicht oseits am besten Riviera Stücken, nur dass das Apicalauge stets deutlich weiss gekernt ist. Die Vlf. — Us. zeigt ein mattes Braungelb mit sehr schmalen Randfeld. Die Hfl. — Us. ist erdbraun mit kaum sichtbarer Mittellinie. 4 bis 5 gelbbraun umzogene Augen sind stets vorhanden. Beim ♀ sind auf der Os. die leuchtend gelbbraunen Flecke breit angelegt und um das auffallend grosse Apicalauge stark gelblich aufgehellt. Die Ausdehnung der gelbbraunen Flecke entspricht ungefähr der ssp. *hispulla* Hbn. Die Grf. der Vfl. — Us. entspricht der Os. Ein zweites ungekerntes Apicalauge tritt daselbst einzeln auf. Die Grf. der Hfl. ist schokoladebraun mit violetter Einschlag (feilbraun). Unmittelbar nach der schwarzbraun abgesetzten Mittellinie liegen gelbliche Schuppenpartien, denen dann eine breite hellviolettbraune Binde folgt. Die Randbinde ist wiederum gleich dem Innenteil. Die Punktaugen sind sehr klein und schwankt deren Zahl von 0—3. Ein ♀ linksseitig asymmetrisch stark verdunkelt. ♂ u. ♀



Map. 7. The geographical forms, races and sub-species of *Maniola jurtina*. 1. *iernea*; 2. *cassiteridum*; 3. *cantabrica*; 4. *fortunata*; 5. *bispulla*; 6. *by-* *peribispulla*; 7. *emibispulla*; 8. *corfiobispulla*; 9. *megala*; 10. *maraschi*; 11. *iranica*

50—55 mm. Mit der ssp. *megala* Obth. aus dem südlichen Amanus die Marasform nichts gemein."

Diagnostic. The extension of the female upperside fulvous being "closest to *hispulla*" puts this race on its own in the east.

Range. Known only from Marasch.

Discussion. The very restricted locality of *maraschi* and the fact, that no further contribution to its distribution, variation or nature has been made in the literature, as far as I can trace, makes assessment of this race difficult. It is placed as a subspecies of *megala* by Tauber (1970).

race *strandiana* Obratzsov

Maniola jurtina strandiana Obratzsov, 1936: 638—639.

Type locality. Funduklejevka, Kiev, U.S.S.R.

Genitalia. Eastern.

Description. Obratzsov, 1936.

Diagnostic. Larger and fulvous more extensive than the more northern *janira* with which it forms a cline.

Range. Southern Russia — Kiev, Kherson, Crimea, Podolia and Bessarabia, probably Transsylvania: also in east Russia (Vjatka, Malmyzh) and possibly other regions south and west to the Caucasus, forming a cline in Estonia and Novgorod.

Discussion. The differences between *strandiana* and the southern races with eastern type genitalia further west (*prae-* and *emihispulla*) are not too clear and require further investigation.

race *phormia* Fruhstorfer

Epinephele jurtina phormia Fruhstorfer, 1909: 121.

Type locality. Meran, South Tyrol — Fruhstorfer, 1909.

Genitalia. Eastern.

Description. Verity, 1953: 270.

Diagnostic. Differs from *janira* in its larger size and rather more extensive fulvous on the female upperside.

Range. Northern and central Italy from 1.000—1.300 meters. Probably similar forms occur in the Balkan Peninsula and western Turkey.

Discussion. The race *phormia* is the first stage in a cline to the southern forms *prae-hispulla* and *emihispulla*. The differences between this race and *janira* are not great or consistent.

race *prae-hispulla* Verity

Epinephele jurtina race *prae-hispulla* Verity, 1921: 210.

Type locality. Florence — Verity, 1921.

Genitalia. Eastern.

Description. Verity, 1921.

Diagnostic. The larger size and fairly consistent fulvous suffusion on the female upperside hindwing are the only distinguishing features of this race.

Discussion. This race represents no more than a development of race *phormia*. Whether such minor distinctions are worth recognising is open to question.

form *parvula* Stauder

Epinephele jurtina hispulla f. *parvula* Stauder, 1915: 1, pl. 2, fig. 16.

Type locality. Monte Fiato and S. Angelo — Stauder, 1915.

Genitalia. Presumably eastern.

Description. Stauder, 1915.

Range. Found by Stauder only at Monte Fiato and St. Angelo (800—1300 m).

Discussion. Although it is feasible that there exists in this part of Italy a race consisting of dwarf *jurtina*, I would think it more likely, that the sample taken (only four males) in (?) 1914 were characteristic of that year only. Races of very small size of *jurtina* are known (Isle of Man; southwest Sweden).

form *schweigeri* Tauber

Maniola jurtina schweigeri Tauber, 1970: 111—112.

Type locality. Ulu Dag, Bursa, c. 1800 m.

Genitalia. Eastern type *a* (from few specimens).

Description. Tauber, 1970.

Range. Only in the type locality.

Discussion. This race is described on the evidence of the male genitalia. No females were found or examined. As has been stated the eastern type *a* valve has been found in various scattered localities as far apart as north Italy, Crete and U.S.S.R. Consequently, I do not believe that *schweigeri* should be recognised as a geographical race.

Maniola jurtina emihispulla Verity

Epinephele jurtina race *emihispulla* Verity, 1919: 124.

Type locality. Poggio, Elba — Verity, 1919.

Genitalia. Eastern with some transitional forms.

Description. Verity, 1953: 269.

Diagnostic. The fairly extensive female fulvous on the upperside is distinctive.

Range. Elba, Corsica and perhaps the far south of Italy. The form in some localities in the Maritime Alps (e.g. Col du Tende) is probably best placed with this sub-species.

Discussion. This is the only race with eastern type genitalia which makes any real approach to the fulvous marking found in *hispulla*. Even this is, however, not consistent and the underside medial line on the forewing is characteristically eastern.

Maniola jurtina corfiothispulla Graves

Maniola jurtina corfiothispulla Graves, 1933: 180.

Type locality. Corfu — Graves, 1933.

Genitalia. Eastern.

Description. Graves, 1933.

Diagnostic. The large size of both sexes, dully coloured upperside of the male and

peculiar fulvous colour in the female, serve to distinguish this race.

Range. Known only from Corfu and Crete.

Discussion. It is likely that *corfiotispulla* will be found on other Greek islands, where conditions have favoured its evolution.

Maniola jurtina persica Le Cerf

Epinephele jurtina var. *persica* Le Cerf, 1912: 227.

Type locality. Iran (Tidar, Cazevin, Hamadan, Kohroud) — Le Cerf, 1912.

Genitalia. Eastern.

Description. Le Cerf, 1912: 227 (illustrated by Le Cerf, 1913: pl. II, figs. 16, 17).

Diagnostic. See Le Cerf, 1913: 42—43.

Range. Plateau of Iran, Kurdistan and northeast Turkey.

Discussion. The differences between *persica*, *strandiana* and other eastern races require to be defined much more clearly.

ghilanica-group

Maniola jurtina ghilanica Le Cerf

Epinephele jurtina var. *persica* Le Cerf, 1912: 227.

Type locality. Ghilan: Seilan-Kelahé, Seng-e-Serek, Sia-Khâni — Le Cerf, 1913.

Genitalia. Primitive.

Description. Le Cerf, 1913. Male — 50.3 mm (smallest 49.0: largest 52.0); upperside: forewing fulvous scaling orange suffuse and variable usually confined to a ring around the apical eyespot. Apical eyespot moderately large and well defined distinctly pupilled. Androconial band well defined not extending beyond vein three. Hindwing without fulvous scaling; underside: forewing basal and discal areas light fulvous barely distinguishable from the submarginal band usually with no medial line. Outer margin and termen greyish almost without striae. Apical eyespot moderately large single pupilled. Hindwing basal and discal areas greyish brown. Medial band very slightly lighter, usually with two to four ocelli, unpupilled and encircled with fulvous. Wing almost without striae;

Female — 56.3 mm (smallest 55.0: largest 58.0); upperside: ground colour dark. Forewing fulvous scaling orange present as a suffuse patch in the discal area. Submarginal band fairly extensive, not broken by the ground colour along the nervures. Apical eyespot rather small, sometimes bipupilled. Hindwing with occasional submarginal fulvous; underside: forewing basal and discal areas light reddish fulvous, contrasting with the lighter submarginal band with an indistinct medial line. Outer margin and termen greyish brown fulvous, darker basally, fairly strongly striate. Apical eyespot moderately large, sometimes bipupilled. Hindwing basal and discal areas outer margin rather dark grey or brown fulvous. Medial band silvery or violet grey without ocelli. Wing rather strongly striate.

Variation is largely confined to the extent of fulvous in both sexes and the size of the female apical eyespot. The underside of the female is remarkably constant.

Diagnostic. By the smaller size and colouration of the underside in both sexes, this sub-species differs from the only other sub-species with primitive genitalia.

Range. The northern watershed of the Elburz Mountains, Iran, at least as far west as Cala-dagli in the far east of Turkey.

Diagnostic. By the smaller size and coloration of the underside in both sexes, this indeed it would indicate that my series belonged to a different race. However, the original description was based on only four males and one female. It is possible that in this region, at the edge of the *jurtina* range, the populations are so isolated, that some have evolved their own characteristics, in spite of the fact that these populations are probably more homogeneous than *jurtina* anywhere in the west.

Maniola jurtina iranica subsp. nov.

Holotype. Male — Ab-e-Ali, Teheran, Iran (2200 m) 4 July, 1970, J. H. Robert. Paratypes. 1 male — data as holotype, 4 females — data as holotype. Holotype and paratypes in the author's collection.

Genitalia. Primitive.

Description. Male — 54.5 mm (smallest 54.0: largest 55.0); upperside: forewing fulvous scaling yellowish confined to a ring around the eyespot. Apical eyespot moderately large, fairly well defined and distinctly pupilled. Androconial band rather well defined, not extending beyond vein three. Hindwing without fulvous scaling; underside: forewing basal and discal areas light fulvous, almost indistinguishable from the submarginal band, with a very indistinct medial line. Outer margin and termen light greyish without striae. Apical eyespot moderately large, single pupilled. Hindwing basal and discal areas and outer margin light greyish, medial band barely lighter, usually with two unpupilled ocelli, encircled with fulvous. Wing without striae. Female — 59.6 mm (smallest 58.0: largest 62.0); upperside: ground colour light. Fulvous scaling yellowish, present as a suffuse patch in the discal area. Submarginal band well defined, occasionally broken by the ground colour along the nervures. Apical eyespot large, often bipupilled. Hindwings with occasional suffuse submarginal fulvous. Underside: forewing basal and discal areas light fulvous, contrasting with the lighter submarginal band, with a very indistinct medial line. Outer margin and termen light yellowish grey, darker inwardly without striae. Apical eyespot rather large, often bipupilled. Hindwing basal and discal areas and outer margin light yellowish grey. Medial band lighter, with 0—3 very small unpupilled ocelli. Wing without striae.

Variation is in the extent and form of the female upperside fulvous which may be broken, or not by the ground colour along the nervures and the size of the apical eyespot which is occasionally very large. The female underside is virtually constant.

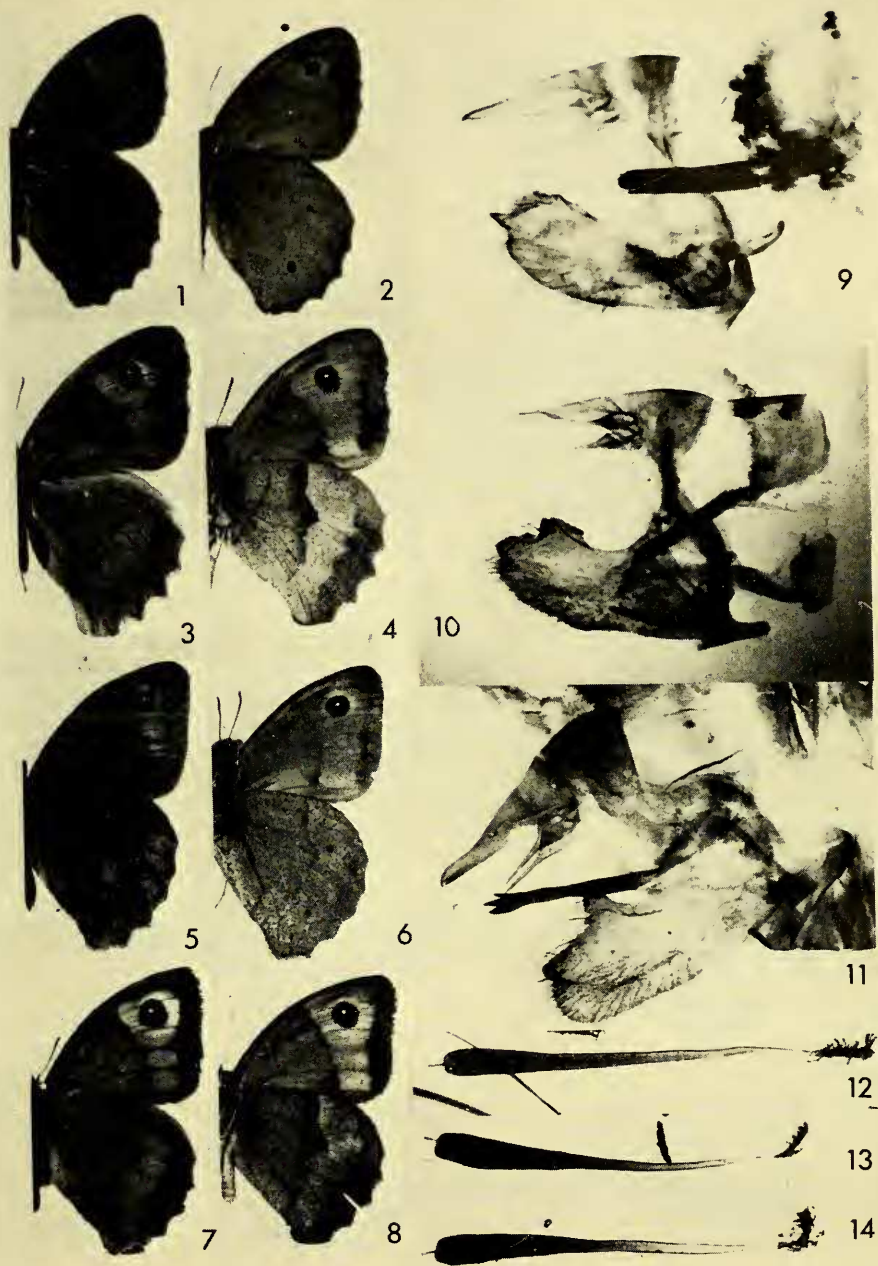
Diagnostic. Differs from *ghilanica* in its large size and by the pale light fulvous of the underside forewing and pale coloration of the hindwing in the female.

Range. The dry southern slopes of the Elburz Mountains and probably reaching across north Iran to north east Turkey.

Discussion. The report by De Lattin (1950: 318) of ssp. *persica* at Van, Tatvan, Rasa-diye and Sasan-daglari in northeast Turkey probably refers to this race. The markings of *iranica* are possibly closer to *persica* than *ghilanica*.

LIST OF NAMES ASSOCIATED WITH *Maniola jurtina* L.

<i>addenda</i> Mousley	<i>fulvopincta</i> Heinrich	<i>nana</i> Stephen
<i>alba</i> Blackie	<i>ghilanica</i> Le Cerf	<i>nigrianira</i> Forsyth-Johnstone
<i>antalyana</i> Tauber	<i>glabrata</i> Leeds	<i>nigro-rubra</i> Lambillion
<i>anticrassipuncta</i> Leeds	<i>grisea</i> Tutt	<i>nuragiformis</i> Verity
<i>antifulva</i> Leeds	<i>grisea-argentacea</i> Oberthür	<i>obliterans</i> Seitz
<i>antiparvipunctata</i> Leeds	<i>bertha</i> Heinrich	<i>oblitiscens</i> Schultz
<i>antipluripunctata</i> Leeds	<i>bispulla</i> Esper	<i>occidentalis</i> Pionneau
<i>antirufa</i> Leeds	<i>bispulla</i> Hübner	<i>ocellata</i> Tutt
<i>antiultrafulvescens</i> Leeds	<i>buenei</i> Krulikovsky	<i>pallens</i> Thiery-Mieg
<i>anomala</i> Rebel	<i>hyperanthoides</i> Thomson	<i>pallidus</i> Frohawk
<i>anommata</i> Verity	<i>hyperbispulla</i> Thomson	<i>pamphilus</i> Hoefnagel
<i>apicoextensa</i> Leeds	<i>iernes</i> Graves	<i>parafeminea</i> Thomson
<i>biocellata</i> Lempke	<i>ierniformis</i> Graves	<i>parvula</i> Stauder
<i>biocellata</i> Tutt	<i>illuminata</i> Krulikovsky	<i>pauper</i> Verity
<i>biocullata</i> Rebel	<i>illustris</i> Jachontoff	<i>persica</i> Le Cerf
<i>brevipennis</i> Lempke	<i>infra-impunctata</i> Leeds	<i>phormia</i> Verity
<i>brigitta</i> Ljunch	<i>infrapupillata</i> Lempke	<i>postexcessa</i> Leeds
<i>caeca</i> Ksenschopolski	<i>infrareticulata</i> Lempke	<i>praeispulla</i> Verity
<i>caeca</i> Rebel	<i>inocellata</i> Kiss	<i>pseudomas</i> Cockerell
<i>caecoides</i> Strand	<i>insularis</i> Thomson	<i>radiata</i> Frohawk
<i>cantabrica</i> Agenjo	<i>intermedia</i> Blackie	<i>rectoformis</i> Thomson
<i>cassiteridum</i> Graves	<i>iranica</i> Thomson	<i>rufocincta</i> Fuchs
<i>cervinus</i> Frohawk	<i>janira</i> Linnaeus	<i>schweigeri</i> Tauber
<i>cinerascens</i> Fuchs	<i>janirus</i> Herbst	<i>semialba</i> Brand
<i>cinerea</i> Cosmovici	<i>jurtina</i> Linnaeus	<i>semi-intermedia</i> Lempke
<i>coeca</i> Rocci	<i>latimargo</i> Peerdeman	<i>splendida</i> Buchanan White
<i>commacula</i> Leeds	<i>lemur</i> Schrank	<i>strandiana</i> Obratzsov
<i>concolorata</i> Thomson	<i>leucothoë</i> Cabeau	<i>subbispulla</i> Strand
<i>corfiothispulla</i> Graves	<i>luigionii</i> Rostagno	<i>subtus-albida</i> Silbernagel
<i>costa-cava</i> Cabeau	<i>major</i> Leeds	<i>suffusa</i> Tutt
<i>dextro-albescens</i> Tutt	<i>maraschi</i> Pfeiffer	<i>telmessiaeformis</i> Verity
<i>emibispulla</i> Verity	<i>marginata</i> Thomson	<i>testacea</i> Schille
<i>erymanthea</i> Esper	<i>marmorea</i> Lambillion	<i>tincta</i> Blackie
<i>erymanthoides</i> Strand	<i>megala</i> Oberthür	<i>tithoniformis</i> Verity
<i>feminea</i> Graves	<i>meridionalis</i> Pionneau	<i>ubryki</i> Aigner
<i>fortunata</i> Alpheraky	<i>mirtyllus</i> Fourcroy	<i>violacea</i> Wheeler
<i>fracta</i> Zweigelt	<i>miscens</i> Verity	<i>wautieri</i> Lambillion
<i>frohawki</i> Blackie	<i>monoculus</i> Goeze	



Pl. 1. Fig. 1, 2 — *Maniola jurtina iranica*, male holotype. Fig. 3, 4 — *Maniola jurtina iranica*, female paratype. Fig. 5, 6 — *Maniola jurtina hyperbispulla*, male holotype. Fig. 7, 8 — *Maniola jurtina hyperbispulla*, female paratype. Fig. 9 — male genitalia, primitive type (Iran). Fig. 10 — male genitalia, eastern type (U.S.S.R.). Fig. 11 — male genitalia, western type (Spain). Fig. 12 — androconial scale, Morocco. Fig. 13 — androconial scale, Crete. Fig. 14 — androconial scale, Iran. (Fig. 1—8 Slightly reduced, Fig. 9—11 $\times 15$, Fig. 12—14 greatly magnified)